JHR 94: 13–88 (2022)
doi: 10.3897/jhr.94.94263
https://jhr.pensoft.net

RESEARCH ARTICLE

JOURNAL OF Hymenoptera RESEARCH
A peer-reviewed open-access journal
The International Society of Hymenopterists

From hell's heart I stab at thee! A determined approach towards a monophyletic Pteromalidae and reclassification of Chalcidoidea (Hymenoptera)

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Academic editor: Miles Zhang | Received 31 August 2022 | Accepted 24 October 2022 | Published 20 December 2022

https://zoobank.org/6CB80723-9A47-403F-ABEC-9AF8AE7F417F

Citation: Burks R, Mitroiu M-D, Fusu L, Heraty JM, Janšta P, Heydon S, Papilloud ND-S, Peters RS, Tselikh EV, Woolley JB, van Noort S, Baur H, Cruaud A, Darling C, Haas M, Hanson P, Krogmann L, Rasplus J-Y (2022) From hell's heart I stab at thee! A determined approach towards a monophyletic Pteromalidae and reclassification of Chalcidoidea (Hymenoptera). Journal of Hymenoptera Research 94: 13–88. https://doi.org/10.3897/jhr.94.94263

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Abstract

The family Pteromalidae (Hymenoptera: Chalcidoidea) is reviewed with the goal of providing nomenclatural changes and morphological diagnoses in preparation for a new molecular phylogeny and a book on world fauna that will contain keys to identification. Most subfamilies and some tribes of Pteromalidae are elevated to family level or transferred elsewhere in the superfamily. The resulting classification is a compromise, with the aim of preserving the validity and diagnosability of other, well-established families of Chalcidoidea. The following former subfamilies and tribes of Pteromalidae are elevated to family rank: Boucekiidae, Ceidae, Cerocephalidae, Chalcedectidae, Cleonymidae, Coelocybidae, Diparidae, Epichrysomallidae, Eunotidae, Herbertiidae, Hetreulophidae, Heydeniidae, Idioporidae, Lyciscidae, Macromesidae, Melanosomellidae, Moranilidae, Neodiparidae, Ooderidae, Pelecinellidae (senior synonym of Leptofoeninae), Pirenidae, Spalangiidae, and Systasidae. The following subfamilies are transferred from Pteromalidae: Chromeurytominae and Keiraninae to Megastigmidae, Elatoidinae to Neodiparidae, Nefoeninae to Pelecinellidae, and Erotolepsiinae to Spalangiidae. The subfamily Sycophaginae is transferred to Pteromalidae. The formerly *incertae sedis* tribe Lieparini is abolished and its single genus *Liepara* is transferred to Coelocybidae. The former tribe Tomocerodini is transferred to Moranilidae and elevated to subfamily status. The former synonym Tridyminae (Pirenidae) is treated as valid. The following former Pteromalidae are removed from the family and, due to phylogenetic uncertainty, placed as *incertae sedis* subfamilies or genera within Chalcidoidea: Austrosystasinae, Ditropinotellinae, Keryinae, Louriciinae, Micradelinae, Parasaphodinae, *Rivasia*, and Storeyinae. Within the remaining Pteromalidae, Miscogastrinae and Ormocerinae are confirmed as separate from Pteromalinae, the former tribe Trigonoderini is elevated to subfamily status, the former synonym Pachyneurinae is recognized as a distinct subfamily, and as the senior synonym of Austroterobiinae. The tribe Termolampini is synonymized under Pteromalini, and the tribe Uzkini is synonymized under Colotrechnini. Most former Otitesellinae, Sycoecinae, and Sycoryctinae are retained in the tribe Otitesellini, which is transferred to Pteromalinae, and all other genera of Pteromalinae are treated as Pteromalini. Eriaporidae is synonymized with Pirenidae, with Eriaporinae and Euryischiinae retained as subfamilies. Other nomenclatural acts performed here outside of Pteromalidae are as follows: Calesidae: elevation to family rank. Eulophidae: transfer of Boucekelimini and Platytetracampini to Opheliminae, and abolishment of the tribes Elasmini and Gyrolasomyiini. Baeomorphidae is recognized as the senior synonym of Rotoitidae. Khutelchalcididae is formally excluded from Chalcidoidea and placed as *incertae sedis* within Apocrita. Metapelmatidae and Neanastatidae are removed from Eupelmidae and treated as distinct families. *Eopelma* is removed from Eupelmidae and treated as an *incertae sedis* genus in Chalcidoidea. The following subfamilies and tribes are described as new: Cecidellinae (in Pirenidae), Enoggerinae (*incertae sedis* in Chalcidoidea), Erixestinae (in Pteromalidae), Eusandalinae (in Eupelmidae), Neapterolelapinae (*incertae sedis* in Chalcidoidea), Solenurinae (in Lyciscidae), Trisecodinae (in Systasidae), Diconocarini (in Pteromalidae: Miscogastrinae), and Trigonoderopsini (in Pteromalidae: Colotrechninae). A complete generic classification for discussed taxa is provided.

Keywords

New family, taxonomic change

"Towards thee I roll, thou all-destroying but unconquering whale; to the last I grapple with thee; from hell's heart I stab at thee"

Herman Melville, "Moby Dick"

Introduction

Pteromalidae as defined by Bouček (1988), contains 33 subfamilies and approximately 640 genera, by far the largest count in Chalcidoidea of both categories. However, there has been agreement for decades (Heraty and Darling 1984; Noyes 1990; Gibson et al. 1999) that Pteromalidae has been a polyphyletic "dumping ground" of taxa that do not obviously fit within previously established families of Chalcidoidea. Because of the highly varied morphology and life histories of taxa contained in Pteromalidae, the family has no unifying features. This narrative is complicated by the highly varied morphology and life histories present in the largest pteromalid subfamily, Pteromalinae, which contains by far the most genera and includes parasitoids of hosts across holometabolous insects, and also egg parasitoids of Hemiptera, predators in spider egg sacs, hyperparasitoids and gall-makers. Just as Pteromalidae has not been recently defined in a way that excludes other chalcidoids, the subfamily Pteromalinae, with approximately 315 genera (Noyes 2019) before the publication of this article, has also not been recently diagnosed in a way that excludes other pteromalids. This is presumably because the diversity of Pteromalinae makes definition exceedingly difficult (Graham 1969; Bouček 1988).

The lack of easy characterization of the subfamily Pteromalinae may have contributed to the eventual dumping-ground nature of the family Pteromalidae, but the greatest contributor may instead be the nature of the subfamily Cleonyminae, which contains many morphologically generalized parasitoids of wood-boring beetles. Bouček (1988) indicated that many pteromalid subfamilies could intuitively be derived from early cleonymine-like stock. However, if this early stock is made up entirely of species classified as Cleonyminae, it would cause the subfamily to be paraphyletic.

Inherent in this concept of Pteromalidae is the conclusion that Cleonyminae and Pteromalinae are more closely related to one another than to other Chalcidoidea. However, molecular data have never linked them nor any part of them in a monophyletic group that did not also include most of the other families of Chalcidoidea (Campbell et al. 2000; Munro et al. 2011; Heraty et al. 2013). This does not indicate that Bouček (1988) was incorrect in his hypothesis, but instead allows the possibility that much of the rest of Chalcidoidea outside Pteromalidae may have also been derived from an assemblage of the early cleonymine-like stock that he postulated. Under this scenario, a researcher wishing to find the sister group of almost any distinctive family in Chalcidoidea is forced to consider the possibility that it may be hidden away among the many obscure subfamilies of Pteromalidae or even within one of their tribes.

An arguably generalized part of the early cleonymine-like stock mentioned by Bouček (1988) may be represented in the Cretaceous by Diversinitidae, an extinct family distinguished from most other chalcidoids, but not from Mymaridae, by having multiporous plate sensilla on the true 1st flagellomere (Haas et al. 2018). Given that Mymaridae is hypothesized as the sister group of other Chalcidoidea (Gibson et al. 1999; Munro et al. 2011; Heraty et al. 2013), Diversinitidae may also be part of the outgroup relative to most other Chalcidoidea. Also, given that Diversinitidae are otherwise not particularly unusual relative to most other Chalcidoidea, especially

being similar in habitus to the pteromalid subfamilies Pteromalinae or Louriciinae, it is possible that morphological diagnoses of family-rank lineages from within Pteromalidae will require greater focus upon relatively subtle features that have been previously overlooked or rejected as indicators of deep phylogenetic splits. It also suggests that an elongate body shape with a large mesopleural area and subtriangular metasoma, that together can be called a "pteromaloid habitus" as seen in Diversinitidae and in pteromalid taxa such as Pteromalinae, Cleonyminae, Colotrechninae, and Pireninae, may not always be indicative of membership in Pteromalidae.

Indeed, many families herein removed from Pteromalidae do not have any known members with the pteromaloid habitus as defined here, and this has been one of the many indicators that subfamilies such as Cerocephalinae, Eunotinae, Herbertiinae, Pelecinellinae (senior synonym of Leptofoeninae), Spalangiinae, and Storeyinae may not be closely related to core Pteromalidae at all. To make matters more confusing, not all core Pteromalinae have the "pteromaloid habitus", in part because of the diverse life histories of pteromalines. The most conspicuous examples of this are the non-pollinating fig wasps, previously classified in three subfamilies treated as Agaonidae, that have been indicated by molecular data to form a monophyletic group within Pteromalidae (Rasplus et al. 1998). This left open the possibility, when examining morphology alone, that some or all of the morphologically distinctive subfamilies mentioned above could be nothing more than apomorphic members of Pteromalidae that have evolved an unusual habitus due to having different life histories. Several molecular studies have been used to test these morphological hypotheses of phylogenetic relationship and support the results being presented herein (Campbell et al. 2000; Munro et al. 2011; Heraty et al. 2013; Cruaud et al., submitted).

Over the time spent on this project, we have seen that analyses using molecular data alone are not always reliable, and that morphological or life history insights can be helpful in discovering contamination events, or even for suggesting that more rigorous phylogenetic analytical methods may be required (Cruaud et al., submitted). The new classification presented here is therefore not simply a reaction to the results of a new molecular phylogeny. Instead, it is the product of a broader analysis in which morphological investigation and knowledge of natural history have played an active role in a process of reciprocal illumination as described by Hennig (1950 1966). The result is a more credible hypothesis of phylogenetic relationships within Chalcidoidea than has been previously seen, with natural and diagnosable higher taxa being proposed here.

In the course of our molecular studies, interesting monophyletic groups have been discovered, including a "Gall Clade" containing previously unassociated taxa that share a gall association: Cynipencyrtidae, Epichrysomallidae new status, Melanosomellidae new status, Ormyridae, and Tanaostigmatidae (Cruaud et al., submitted; van Noort et al., in prep.). Because these families resemble each other mainly in an overall arched body shape and in other features that could have been dismissed as insignificant, these could have been dismissed as the result of convergence due to shared gall association. Instead, a clade has been revealed that can greatly facilitate evolutionary studies of

many chalcidoid gall associates while excluding other gall-associate chalcidoids that have developed this association independently.

This is not to say that other families of Chalcidoidea have been entirely unaffected by our investigations. While the focus of this publication is to outline changes necessary to produce a new, monophyletic Pteromalidae that is more useful for biological research, necessary changes to other families are discussed here as well. In this respect, we have chosen an approach that preserves previously accepted families such as Signiphoridae and Tanaostigmatidae, whereas an alternative approach could have lumped them into larger families that would prove more difficult to diagnose using easily visible morphological features. This is in keeping with the approach used by Zhang et al. (2022), which preserved the previous concept of Eucharitidae by subdividing Perilampidae and treating Eutrichosomatidae, previously a subfamily of the Pteromalidae, as a separate, but related family.

Finally, a number of taxa are kept as *incertae sedis* in Chalcidoidea, based on two criteria. They have either not been analyzed molecularly and/or they cannot currently be placed with certainty in another family or as separate families. This is carried out as the lesser of evils: to avoid creating a potentially unstable family-level classification, we leave some small and obscure taxa as unplaced in Chalcidoidea, pending future analysis. The present treatment calls attention to these otherwise obscure taxa, but it also avoids unnecessary family names that would be synonymized if the data suggest it.

Materials and methods

Morphological terms generally follow Gibson (1997) and Krogmann and Vilhelmsen (2006). Subforaminal bridge terms follow Heraty et al. (2013) or Burks et al. (2015) with the addition of using hypostoma as defined by Mikó et al. (2007). Terms regarding the antennal cleaner complex of the 1st protarsomere, such as the basitarsal comb and basitarsal notch, are defined by Basibuyuk and Quicke (1994). Mandibles are discussed in the plural, because of their frequent and diagnostically useful asymmetry in tooth count. Metatibial spurs are also discussed in the plural, since their count varies from 1 to 2 in many families. For family-group diagnoses, features are only mentioned if they are useful and relevant for distinction from another family. The word funiculars are used to indicate flagellomeres between the anelli and clava. We treat the term frenal line as indicating a space where the frenal groove, or any other transition indicating a frenum, can occur. Given that the frenal line is indicated through various different means in Chalcidoidea, the frenal line itself is mainly mentioned when it is indicated by something other than a groove. Similarly, the axillula can be set off medially by what is called the axillular sulcus or axillular carina, depending upon which component of it is more strongly expressed. To minimize wordiness in diagnoses, if a feature is highly variable or unknown within a given family, it is not mentioned.

Families emerging from Pteromalidae

Boucekiidae new status

Boucekiini Gibson, 2003. Type genus: *Boucekius* Gibson, 2003.

Diagnosis. Antenna with 8 flagellomeres, including a single anellus and an undivided clava. Eyes ventrally divergent. Clypeus without transverse subapical groove. Labrum hidden behind clypeus. Mandibles with ventral tooth and large dorsal truncation. Mesoscutellum with frenum set off by complete frenal groove, and with axillular sulcus (Fig. 1). Mesopleural area without expanded acropleuron; mesepimeron not extending over anterior margin of metapleuron. All legs with 5 tarsomeres; protibial spur stout and curved; basitarsal comb longitudinal; metafemur with ventral lobe or subapical teeth (Fig. 2). Metasoma with epipygium (Fig. 3), or with syntergum (*Chalcidiscelis* Ashmead).

Discussion. Gibson (2003) described Boucekiidae as a new tribe, although it differed from many species in Cleonyminae (as then defined) in the frenum and potentially the labrum. In habitus boucekiids do resemble former Cleonyminae and other large-bodied Chalcidoidea that have metallic coloration. Out of former Cleonyminae, those with an unambiguous frenal arm (= mesoscutellar arm) laterally are now classified in Solenurinae (Lyciscidae), which differ most notably in having an incomplete frenal line and a flagellum with 2 or 3 clavomeres. Chalcedectidae and Heydeniidae can have either an indistinct frenal groove, a small frenum, or a strongly expanded marginal rim of the mesoscutellum that may resemble a frenum; however, both have a different clava from Boucekiidae, with multiple clavomeres instead of an undivided clava and, in Chalcedectidae, an apical spine in females. Chalcedectidae have a syntergum that is not crossed by a transverse sulcus and otherwise does not have an epipygium. Heydeniidae have a long prepectus that is enlarged both laterally and ventrally. The elongate ovipositor and more or less elongate cerci in females may cause confusion with Torymidae or Megastigmidae, both of which have multiple clavomeres and more than 8 flagellomeres. The narrow, essentially parallel-sided flagellomeres may invite confusion with the antenna in Ceidae or Macromesidae; however, members of both these taxa have multiple clavomeres and much narrower mandibles with no dorsal truncation, and Macromesidae lack a frenum. Pteromalidae and Pelecinellidae have more than 1 clavomere in nearly all cases, but Pteromalidae with apparently 1 clavomere (some males) have more than one anelliform basal flagellomere.

Ceidae new status

Ceini Bouček, 1961. Type genus: *Cea* Walker, 1837. Treated as Ceinae by Peck, Bouček and Hoffer (1964).

Diagnosis. Antenna with 12 flagellomeres, including a small 4th clavomere. Eyes not ventrally divergent. Clypeus with transverse subapical groove. Labrum subrectangular

and exposed, with marginal setae in a row (Fig. 4). Mandibles with 2 teeth (Fig. 4). Subforaminal bridge with postgena separated by lower tentorial bridge except for a small postgenal bridge dorsal to the hypostoma. Mesoscutellum with frenum indicated at least laterally, and with axillular sulcus. Mesopleural area without an expanded acropleuron. Propodeum with small and circular spiracle separated by more than its own length from the anterior propodeal margin (Fig. 5). All legs with 5 tarsomeres; protibial spur stout and curved; basitarsal comb longitudinal. Metasoma with syntergum, therefore without epipygium.

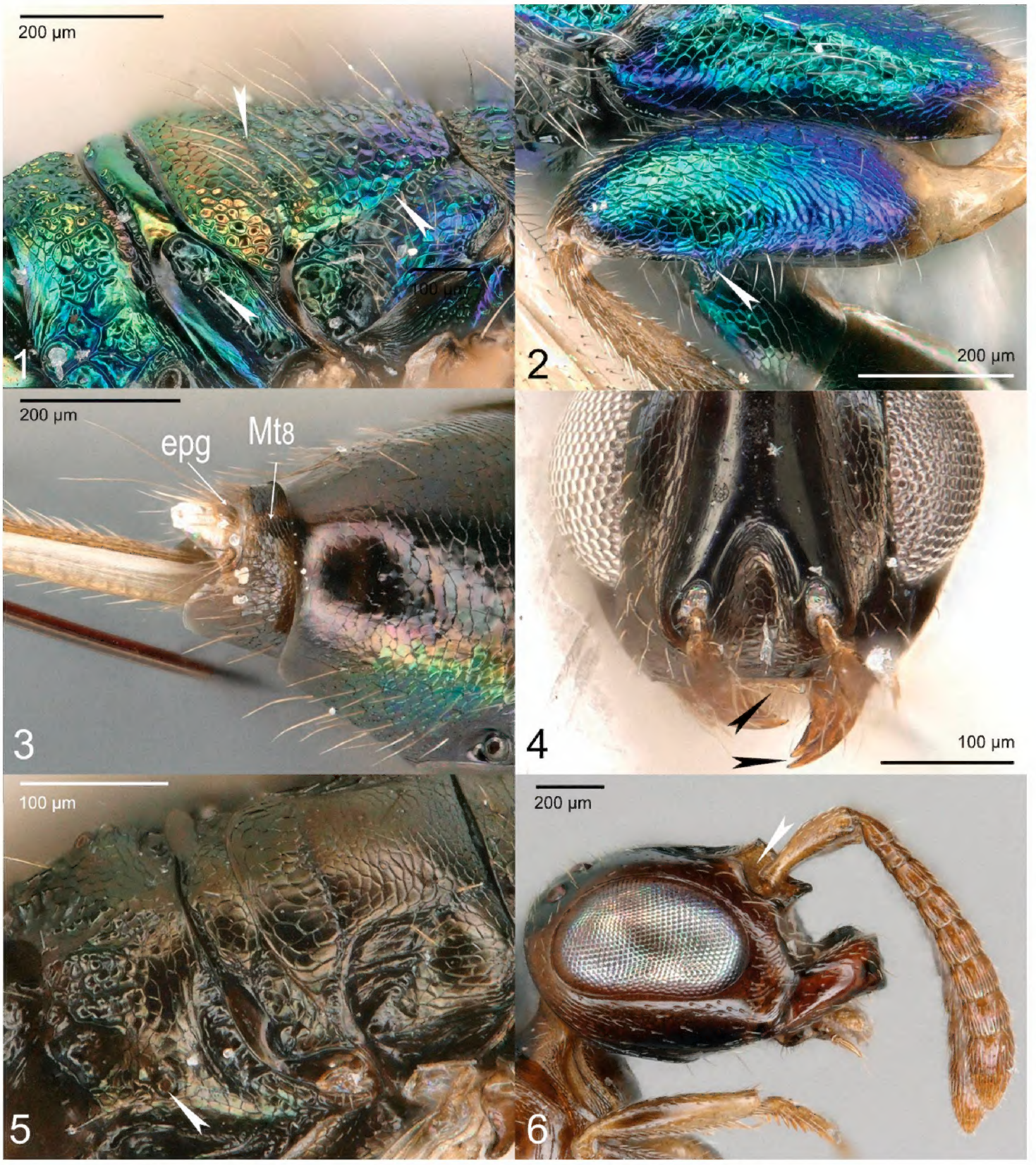
Discussion. Ceidae differs from most other Chalcidoidea in having the propodeal spiracle separated from the anterior propodeal margin by more than its own length. Exceptions to this statement occur in numerous species across many families, including some Pteromalidae. Pteromalidae differ in having more than 2 mandibular teeth except in some fig associates which differ from Ceidae in many other ways. Pteromalidae also lack a transverse subapical clypeal groove, and have a hidden labrum with an elongate median lobe, instead of a subrectangular and exposed labrum. While the subforaminal bridge in Pteromalidae and Ceidae is different, the difference is so slight in many Pteromalidae (such as Colotrechninae and Miscogastrinae) that it should not be relied upon too heavily. Hetreulophidae and the single genus of Macromesidae also have propodeal spiracle separated far from the anterior propodeal margin. Hetreulophidae differ in having distinctly fewer antennal flagellomeres (9), with a single anellus and united clava, and by having 3 mandibular teeth. Macromesidae differ in having only 4 mesotarsomeres in females, at most 11 antennal flagellomeres, and 3 mandibular teeth.

Cerocephalidae new status

Cerocephalinae Gahan, 1946. Type genus: *Cerocephala* Westwood, 1832.

Diagnosis. Antenna with at most 10 flagellomeres and at most 3 clavomeres. Intertorular prominence present (Fig. 6). Eyes not ventrally divergent. Clypeus without transverse subapical groove. Labrum hidden behind clypeus, flexible. Mandibles with 2 or more teeth. Subforaminal bridge with a postgenal bridge occurring dorsal to the hypostoma. Mesoscutellum with frenum indicated at least laterally, although this may be very subtle. Mesopleural area without an expanded acropleuron; mesepimeron extending over anterior margin of metapleuron (Fig. 7). All legs with 5 tarsomeres; protibial spur stout and curved; basitarsal comb longitudinal. Metasoma with syntergum, therefore without epipygium.

Discussion. Cerocephalidae differ from most other Chalcidoidea in having an intertorular prominence, although a few exceptional taxa exist across the superfamily that have a similar prominence, such as some Haltichellinae (Chalcididae). However, these exceptions can be distinguished from Cerocephalidae using other features mentioned in the diagnosis. Otherwise, Cerocephalidae bear little resemblance to other families, being somewhat similar to Spalangiidae, Storeyinae, and some Eulophidae, but without most diagnostic features of those families.



Figures 1–6. 1–3 *Boucekius* sp. (Boucekiidae) **1** metascutellum, axillula and propodeum **2** hind femur **3** epipygium (epg) and metasomal terga VIII (Mt8) **4, 5** *Spalangiopelta* sp. (Ceidae) **4** clypeus, labrum and mandible **5** metascutellum, axillula and propodeum, arrow shows the propodeal spiracle far separated from the anterior propodeal margin **6** *Muesebeckisia mandibularis* Hedqvist (Cerocephalidae): head and antenna in lateral view, arrow indicating intertorular prominence.

Chalcedectidae new status

Chalcedectinae Ashmead, 1904. Type genus: *Chalcedectus* Walker, 1852.

Diagnosis. Antenna with 11 flagellomeres, including 3 clavomeres, clava with apical spine in females (Fig. 8). Eyes ventrally divergent. Labrum exposed, sclerotized.

Mandibles with 3 teeth. Subforaminal bridge with a postgenal bridge occurring dorsal to the hypostoma, with convergent hypostomal carina, without a postgenal groove or postgenal lamina. Prepectus with dorsal margin at least as long as tegula. Notauli complete; tegula not covering most of humeral plate. Mesoscutellum with variable frenal area: either without a frenum, or having an expanded marginal rim of the mesoscutellum, or with either a frenum indicated mainly by a frenal arm and an indistinct frenal groove, or an ambiguous frenum that can be difficult to interpret; and with axillular sulcus or carina (Fig. 9). Mesopleural area without an expanded acropleuron; mesepimeron not extending over anterior margin of metapleuron (Fig. 9). All legs with 5 tarsomeres; protibial spur stout and curved; basitarsal comb longitudinal; metafemur with ventral teeth (Fig. 10), with metatibial spurs arising from a ventroapical projection (not shown) or absent (Fig. 10). Metasoma with syntergum, therefore without epipygium.

Discussion. Chalcedectidae are most likely to be confused with other Chalcidoidea that have a metafemur with ventral teeth, which occurs in various families and isolated genera across the superfamily. Chalcididae differ in having a small prepectus, the dorsal margin of which is shorter than the tegula, and in that the tegula covers most or all of the humeral plate. In Lyciscidae, the metatibial spurs arise from a truncate apical margin of the metatibia. Leucospidae have, in females, unusual ovipositor sheaths that recurve over the gaster and fit in a notch and, in males, a carapace-like gaster with at most 3 separate terga. Pelecinellidae have an elongate petiole with many lateral setae at a right angle to the longitudinal axis of the petiole, whereas in Chalcedectidae the petiole is small and hardly visible from dorsal view. Boucekiidae have a single clavomere, and either an epipygium or a transverse sulcus across the syntergum immediately anterior to the cerci. A few Melanosomellidae have a toothed metafemur, but they either lack an axillular sulcus or carina or have a reduced and incomplete one, and do not have ventrally divergent eyes. Cleonymidae have incomplete notauli. Some Torymidae have ventral metafemoral teeth, but these have a separate epipygium in females and do not have ventrally divergent eyes. In *Liepara* Bouček (Coelocybidae), the frenum is unambiguously visible dorsally, with a pair of strong setae adjacent to the frenal groove. A few Eulophidae can have ventral teeth on the metafemur, but they have 4 tarsomeres on all legs.

Cleonymidae revived status

Cleonymidae Walker, 1837. Type genus: *Cleonymus* Latreille, 1809.

Diagnosis. Antenna with 9 flagellomeres, including usually a single clavomere, which is sometimes vaguely divided into 3 clavomeres in males, and with a subapical finger-like process or spine extending alongside the clava and/or with an additional apical spine in females. Eyes ventrally divergent. Clypeus with transverse subapical groove. Labrum exposed, sclerotized. Mandibles with 2 or 3 teeth (Fig. 11), sometimes with a truncation in place of the dorsal teeth. Subforaminal bridge with a postgenal bridge

dorsal to the hypostoma and separating the lower tentorial bridge from the convergent hypostomal carina, and without a postgenal groove or postgenal lamina. Pronotum without a smooth median longitudinal line or carina. Prepectus with dorsal margin at least as long as tegula. Notauli incomplete. Tegula not covering most of humeral plate. Mesoscutellum without a frenum, although frenal arm visible only laterally immediately anterior to marginal rim of mesoscutellum; without axillular sulcus. Mesopleural area without an expanded acropleuron. All legs with 5 tarsomeres; protibial spur stout and curved; basitarsal comb longitudinal; metafemur with or without ventral teeth, with apical spurs arising from a truncate metatibial apex when the metafemur has ventral teeth (Fig. 12). Metasoma with syntergum, therefore without epipygium.

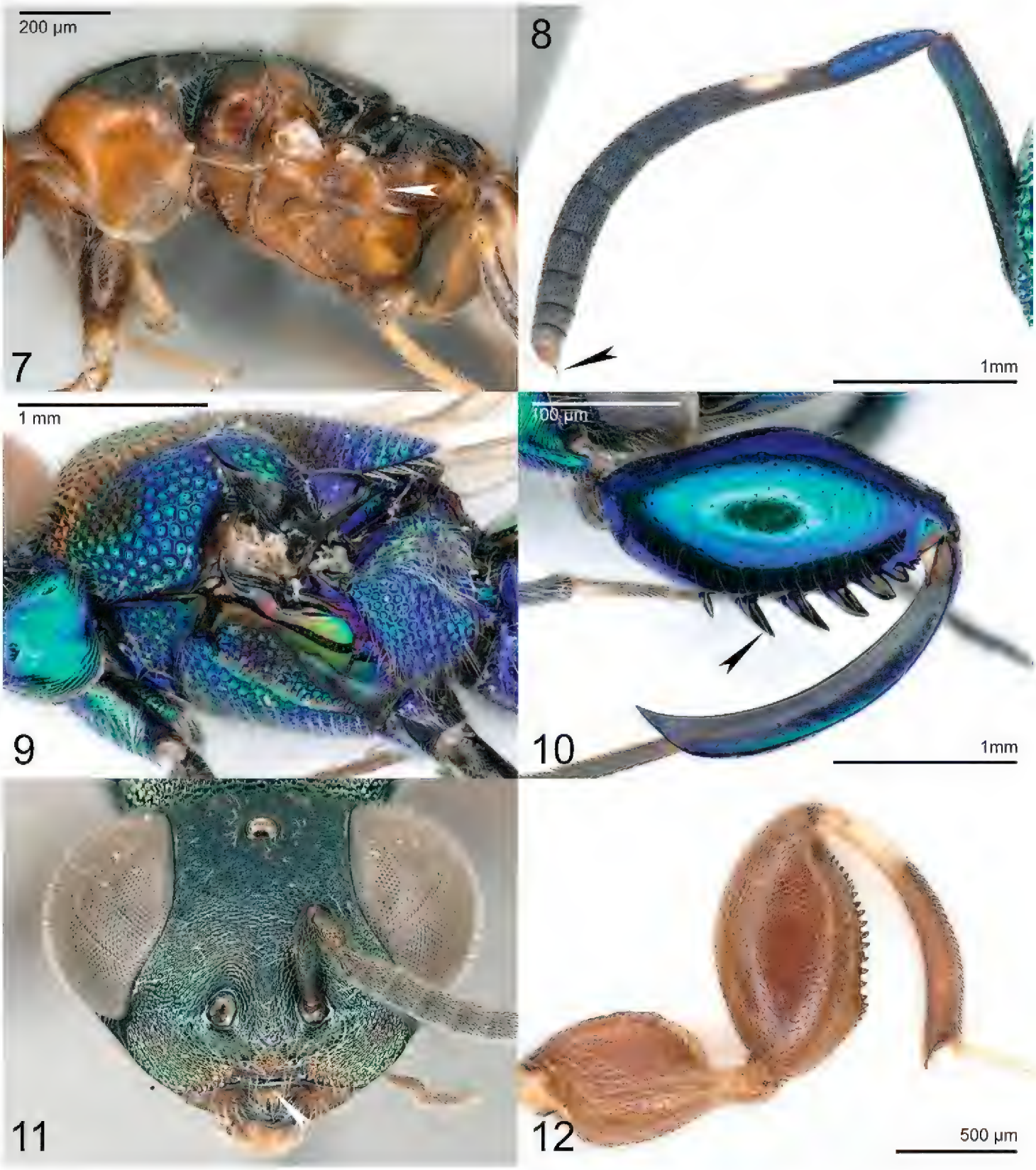
Discussion. Cleonymidae in its current, narrow sense represents the former Cleonymini, as characterized by Gibson (2003). It includes *Agrilocida* Steffan new placement, previously placed in Chalcedectini, but which is distinct morphologically and consistently is placed in Cleonymidae in next-generation molecular analyses. This is now a relatively small and narrowly-defined group in comparison with the previous sense of Cleonyminae, and may be confused with other relatively large-bodied taxa that have ventrally divergent eyes.

Females of Eupelmidae, Metapelmatidae, Neanastatidae, and *Eopelma* Gibson have an enlarged, convex and pad-like acropleuron that covers most or all of the mesopleural area. Lyciscidae, Chalcedectidae, Ooderidae, Pelecinellidae, and Boucekiidae differ from Cleonymidae in having complete notauli. Heydeniidae have a long prepectus with large lateral and ventral surfaces. While some Cleonymidae have ventral teeth on the metafemur, they do not strongly resemble Chalcididae, especially because of the metallic coloration of most Cleonymidae versus the usually non-metallic coloration of Chalcididae, but also because Cleonymidae have incomplete notauli, a larger prepectus, and a smaller tegula that does not cover most of the humeral plate. Coelocybidae usually have non-metallic coloration but also have a distinctive frenum with at least one pair of strong mesoscutellar setae on or nearly adjacent to the frenal groove, whereas the mesoscutellum in Cleonymidae is evenly covered with short and decumbent setae. Additionally, Coelocybidae do not have any spine or finger-like projection on or extending alongside the clava from a previous segment in females.

Coelocybidae new status

Coelocybinae Bouček, 1988. Type genus: *Coelocyba* Ashmead, 1900.
Lieparini Bouček, 1988, new synonymy. Type genus: *Liepara* Bouček, 1988.

Diagnosis. Antenna with 11 flagellomeres. Eyes ventrally divergent. Clypeus with transverse subapical groove (extending from one anterior tentorial pit to the other). Labrum hidden behind clypeus, flexible, subrectangular, with marginal setae in a row. Mandibles with 3 teeth. Subforaminal bridge with postgena separated by



Figures 7–12. 7 *Neocalosoter* sp. (Cerocephalidae): mesosoma in lateral view **8–10** *Chalcedectus* sp. (Chalcedectidae) **8** antenna **9** mesosoma in lateral view **10** hind leg **11** *Cleonymus* sp. (Cleonymidae): head in frontal view **12** *Agrilocida ferrieri* Steffan (Cleonymidae): hind leg.

lower tentorial bridge. Mesoscutellum with frenum indicated and with a pair of strong setae on or adjacent to frenal groove, and with axillular sulcus (Fig. 13). Mesopleural area without an expanded acropleuron; mesepimeron not extending over anterior margin of metapleuron (Fig. 14). All legs with 5 tarsomeres; protibial spur stout and curved; basitarsal comb longitudinal. Metasoma with syntergum, therefore without epipygium.

Discussion. As mentioned by Bouček (1988), Coelocybidae closely resemble what was then known as Cleonyminae, which is now multiple families. Among these, Coelocybidae bear greater resemblance to Cleonymidae and Lyciscidae. Cleonymidae differ from Coelocybidae in lacking a frenum and the accompanying strong setae, the setae also being absent from Lyciscidae. Otherwise, taxa with ventrally divergent eyes have an expanded acropleuron or fewer flagellomeres. Many other taxa have a pair of strong setae on the frenal groove, but not together with ventrally divergent eyes, except *Cecidellis* Hanson (Pirenidae) which has 9 antennal flagellomeres. Nearly all Coelocybidae are from the Southern Hemisphere, with the exception of a single species from India (Narendran 2001).

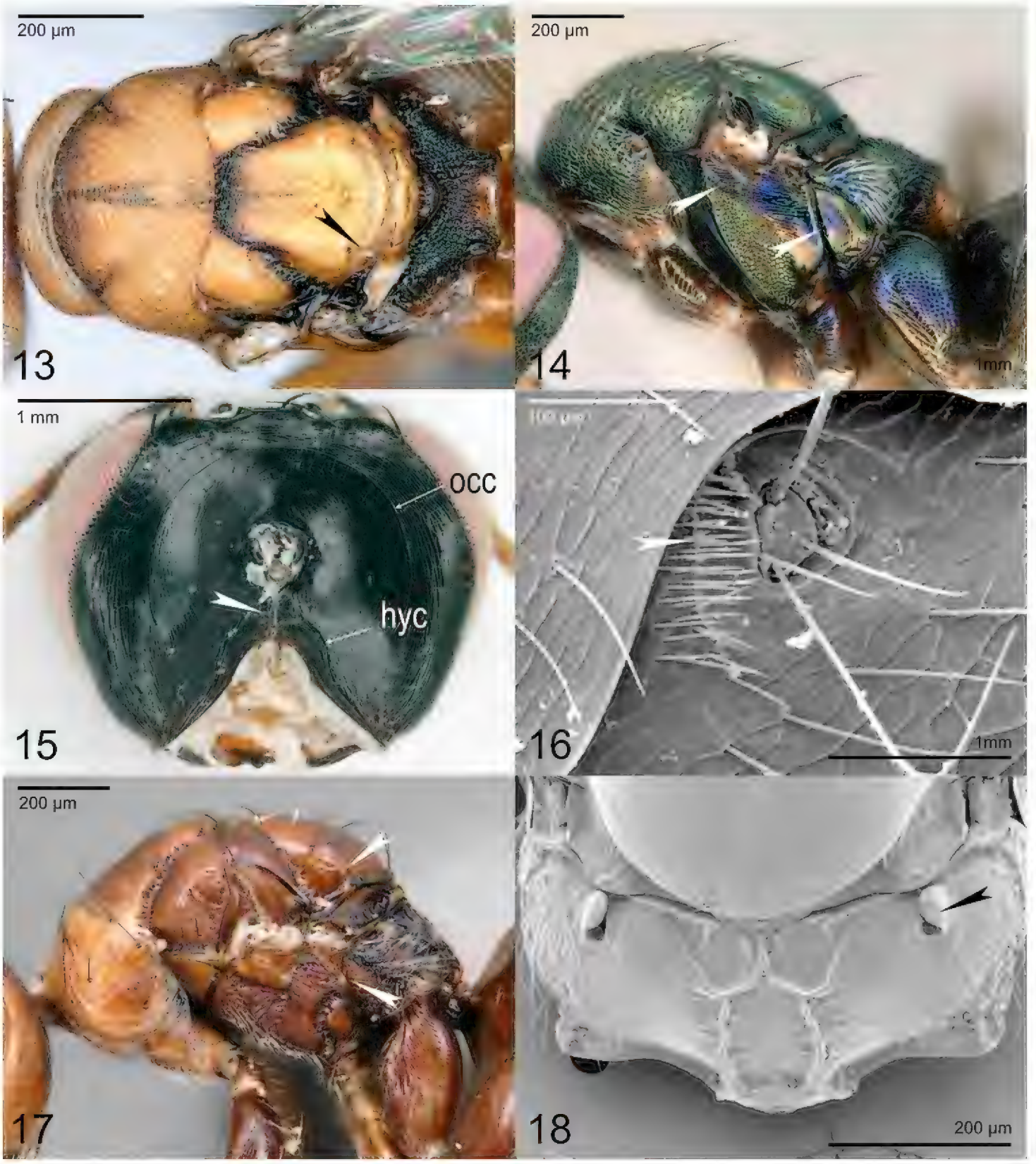
Lieparini new synonym is hereby abolished, and *Liepara* Bouček new placement is transferred here from its *incertae sedis* status (Heraty et al. 2013) because it has consistently been part of the new concept of a monophyletic Coelocybidae in next-generation molecular analyses (Cruaud et al., submitted). While the ventrally toothed metafemur of *Liepara* is distinctive, it is a well-known homoplastic feature in Chalcidoidea. Otherwise, the slightly ventrally divergent eyes, strong setae adjacent to the frenal groove, and non-metallic coloration of *Liepara* indicate that morphology agrees with molecules in this instance. Lieparini does not seem to be a useful tribe to keep as distinct from other coelocybines, although further study may lead to its resurrection once more coelocybids have been analyzed phylogenetically.

Diparidae new status

Diparinae (=Diparides, not Latin) Thomson, 1876. Type genus: *Dipara* Walker, 1833.

Diagnosis. Antenna with 12 flagellomeres, including a small 4th clavomere. Eyes not ventrally divergent. Labrum hidden behind clypeus, flexible, subrectangular, with marginal setae in a row. Mandibles with 3 or 4 teeth. Subforaminal bridge with postgenal bridge occurring dorsal to the hypostoma (Fig. 15). Mesoscutellum with frenum indicated at least laterally, and with axillular sulcus. Mesopleural area without an expanded acropleuron; mesepimeron not extending over anterior margin of metapleuron (except in *Diparisca* Hedqvist). All legs with 5 tarsomeres; protibial spur stout and curved; basitarsal comb longitudinal. Metasoma with syntergum, therefore without epipygium; cercal brush present anterior to cercus (Fig. 16).

Discussion. As discussed by Desjardins (2007), Diparinae have a cercal brush anterior to the cercus (Fig. 16). This feature is not perfectly diagnostic however, because it can also be present in Spalangiidae and Neapterolelapinae, which are recovered as the sister group to Lyciscidae, and Herbertiidae (Cruaud et al., submitted). Spalangiidae differ in having the mesepimeron extending over the anterior margin of the metapleuron. Lyciscidae differ in having an exposed, rigidly sclerotized labrum, and in lacking a frenum (except in Solenurinae). Herbertiidae differ in having at most 10 antennal flagellomeres, and in having an exposed, rigidly sclerotized labrum. In the features



Figures 13–18. 13 *Coelocyboides* sp. (Coelocybidae): mesosoma in dorsal view, arrow indicating setae on or adjacent to frenal groove **14** *Ormyromorpha trifasciata* Girault (Coelocybidae): mesosoma in lateral view **15, 16** *Lelaps* sp. (Diparidae) **15** head posterior view **16** cercal brush **17** *Eufroggattisca polita* (Ashmead) (Epichrysomallidae): mesosoma lateral view **18** *Odontofroggattia* sp. (Epichrysomallidae): propodeum female dorsal view.

listed in the diagnosis, Cerocephalidae may appear similar to Diparidae, although they differ in that Cerocephalidae have an intertorular prominence and at most 10 antennal flagellomeres. *Diparisca* remains in Diparidae as a genus of uncertain placement (Mitroiu 2016), with distinction from Ceinae discussed therein.

Epichrysomallidae new status

Epichrysomallinae Hill & Riek, 1967. Type genus: *Epichrysomalla* Girault, 1915.

Diagnosis. Antenna with 10–12 flagellomeres, including a small 4th clavomere. Eyes not ventrally divergent. Labrum hidden behind clypeus, flexible. Mandibles with 3 teeth. Subforaminal bridge with postgenal bridge separating secondary posterior tentorial pits from hypostoma. Notauli complete. Mesoscutellum with frenum indicated laterally, without axillular sulcus (Fig. 17). Mesopleural area without an expanded acropleuron; mesepimeron extending over anterior margin of metapleuron (Fig. 17). All legs with 5 tarsomeres in most, except tarsi 4-segmented in *Odontofroggatia* Ishii and *Josephiella* Narendran; protibial spur stout and curved; basitarsal comb longitudinal. Metasoma with syntergum, therefore without epipygium.

Discussion. Epichrysomallidae mostly resemble Melanosomellidae in habitus, but do not have a linear mesopleural sulcus. They also have different fore wing venation with a stigmal vein arising at a right angle (excepted in *Acophila* Ishii) and a postmarginal vein that is shorter than the stigmal vein. Epichrysomallidae have a characteristic flap-like expansion of cuticle from the lateral edge of the propodeal spiracle, partially covering the spiracle in dorsal view (Fig. 18) that neither Melanosomellidae nor Ormyridae have. Ormyridae differ further from Epichrysomallidae by having a more conventional fore wing venation, with longer marginal and postmarginal veins, and iridescent coloration in most species.

Eunotidae new status

Eunotinae Ashmead, 1904. Type genus: *Eunotus* Walker, 1834.

Diagnosis. Antenna with at most 11 flagellomeres. Eyes ventrally divergent. Clypeus with transverse subapical groove. Labrum either exposed and well-sclerotized (most species), or hidden behind clypeus (*Epicopterus* Westwood), subrectangular, with marginal setae in a row. Mandibles with 2 or rarely 3 teeth (Fig. 19). Subforaminal bridge with postgena separated by lower tentorial bridge. Pronotum transverse. Mesoscutellum with frenum indicated laterally, with axillular sulcus. Mesopleural area without an expanded acropleuron; mesepimeron not extending over anterior margin of metapleuron; only one mesofurcal pit present (Fig. 20). All legs with 5 tarsomeres; protibial spur stout and curved; basitarsal comb longitudinal (Fig. 21). Metasoma with syntergum, therefore without epipygium.

Discussion. Eunotidae, as defined herein, was previously known as Eunotini (Bouček 1988). Moranilidae, composed of species previously included in Eunotinae, differ in having an oblique basitarsal comb that crosses the area where the basitarsal notch would be, in having pits on the mesopleural area of the mesopectus, and in

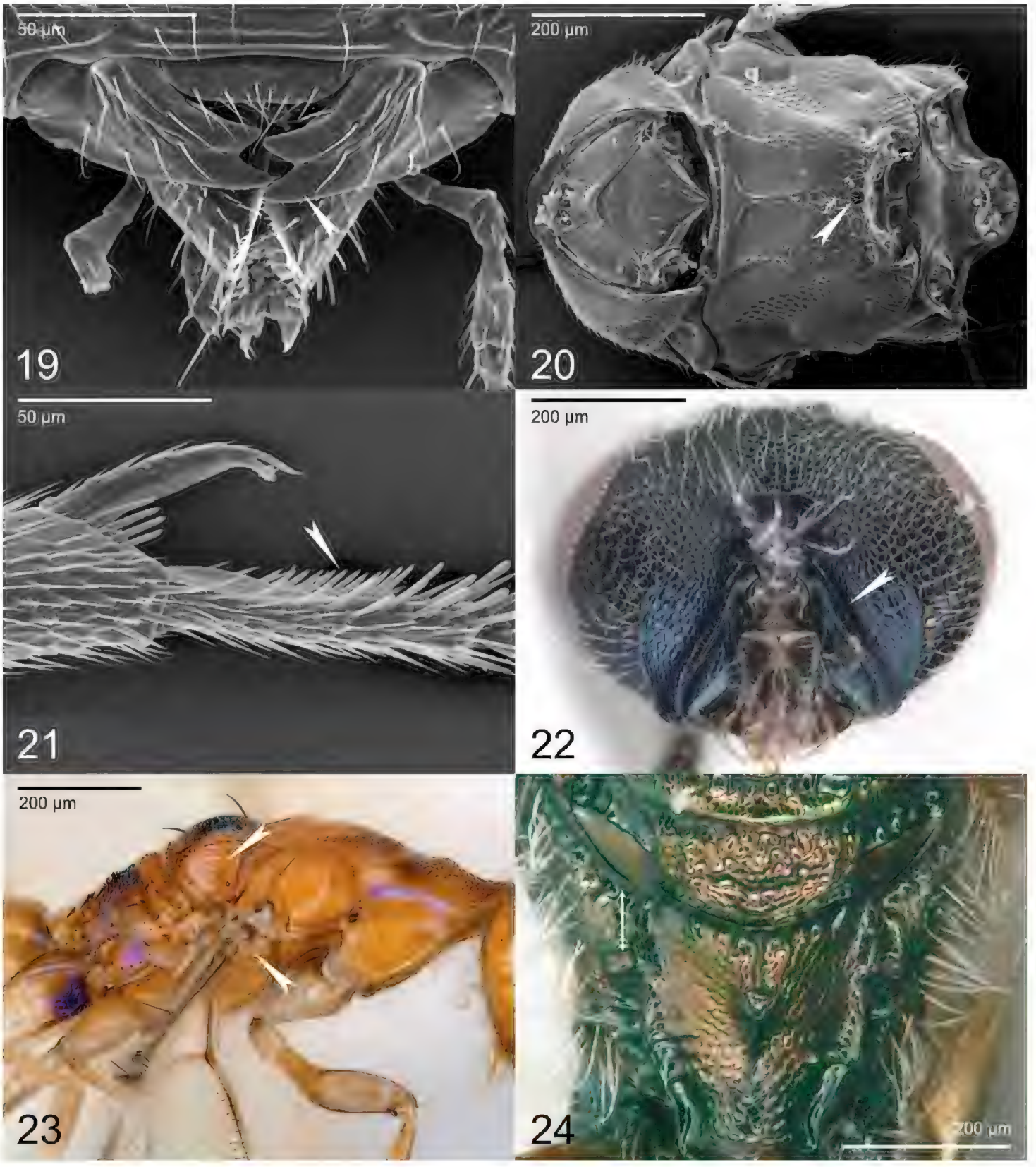
having two mesofurcal pits instead of the single pit usually found in Chalcidoidea. *Idioporus affinis* (Idioporidae) differs in having 4 tarsomeres. Aphelinidae differ in lacking any indication of a frenum, in having a flexible, hidden labrum, usually in having more advanced axilla, and the second phragma extending into the mesosoma. Despite apparent similarities between Aphelinidae and Eunotidae, the two taxa, are seldom confused because Eunotidae have a more strongly sclerotized body, which means that the two families have a very different habitus. Lyciscidae differ in having a subconical pronotum with a median longitudinal carina, whereas the pronotum of Eunotidae is transverse without a visible median carina in dorsal view.

Herbertiidae new status

Herbertiinae Bouček, 1988. Type genus: *Herbertia* Howard, 1894.

Diagnosis. Antenna with 10 flagellomeres, including 3 clavomeres. Clypeus with transverse subapical groove. Labrum exposed, well-sclerotized, subrectangular with marginal setae in a row. Mandibles with 2 teeth. Subforaminal bridge with postgena separated by lower tentorial bridge; head posteriorly with postgenal lamina and postgenal groove (Burks et al. 2018) (Fig. 22). Mesoscutellum with frenum indicated only laterally by the frenal arm, without axillular sulcus. Mesopleural area without an expanded acropleuron, with or without pits. Fore wing marginal vein more than 1.5× stigmal vein length, without elongate uncus. Mesepimeron extending over anterior margin of metapleuron; two mesofurcal pits present. All legs with 5 tarsomeres; protibial spur stout and curved; basitarsal comb oblique. Metasoma with syntergum, therefore without epipygium.

Discussion. The family Herbertiidae has uncertain placement based on both molecular (Cruaud et al., submitted) and morphological data, and is treated as *incertae sedis* in Chalcidoidea pending more consistent phylogenetic resolution. Micradelinae are similar to Herbertiidae in body shape, but differ in having an elongate uncus and much shorter marginal vein relative to the stigmal vein on the fore wing, in having an indicated axillular sulcus, in having only one mesofurcal pit, and in lacking a postgenal lamina and postgenal groove. Erotolepsiinae (Spalangiidae) are similar to Herbertiidae in habitus but differ in having a transverse anterior carina across Gt_1, and in most species having a long carina encircling most of the face. Eunotidae differ in having a longitudinal basitarsal comb, and in lacking a postgenal lamina and postgenal groove. The presence of two mesofurcal pits is unusual, a feature shared with Moranilidae, Enoggerinae, Asaphesinae, some Eurytominae (Krogmann and Vilhelmsen 2006) and Chalcididae (Haltichellinae and Smicromorphinae, G. Delvare, pers. comm). Moranilidae differ in having an axillular sulcus. Other small-bodied families such as Pirenidae and Systasidae differ in having more than 2 mandibular teeth, and Pirenidae differ in having a concealed, flexible labrum.



Figures 19–24. 19–21 *Eunotus* sp. (Eunotidae) **19** mandible and labrum in frontal view **20** mesosoma ventral view **21** protibial spur and basitarsal comb **22** *Herbertia brasiliensis* Ashmead (Herbertiidae) head posterior view **23** *Hetreulophus* sp. (Hetreulophidae), mesosoma lateral view **24** *Zeala walkerae* Bouček (Hetreulophidae): propodeum.

Hetreulophidae new status

Hetreulophini Girault, 1915. Type genus: *Hetreulophus* Girault, 1915.

Diagnosis. Antenna with 9 flagellomeres, including a 1-segmented clava. Clypeus without transverse subapical groove. Labrum flexible, hidden behind clypeus. Mandibles with 3 teeth. Subforaminal bridge with postgena separated by lower tentorial

bridge except for the small postgenal bridge dorsal to the hypostoma. Mesoscutellum with short frenum, with axillular sulcus, and expanded, convex axillula (Fig. 23). Mesopleural area without an expanded acropleuron; mesepimeron extending over anterior margin of metapleuron (Fig. 23). Propodeum with spiracle small, oval, separated by more than its own length from anterior propodeal margin (Fig. 24). All legs with 5 tarsomeres; protibial spur stout and curved; basitarsal comb longitudinal.

Discussion. Ceidae, another family with propodeal spiracle separated far from the anterior margin of the propodeum, differ in having 12 antennal flagellomeres and only 2 mandibular teeth. Macromesidae share this feature as well, but have at least 10 flagellomeres including multiple clavomeres, 4 mesotarsomeres in females, and the mesepimeron does not extend over the anterior margin of the metapleuron. Otherwise, families that resemble Hetreulophidae in habitus have more flagellomeres and multiple clavomeres.

Omphalodipara Girault new placement is transferred from Colotrechninae, Amerostenini (Pteromalidae) to Hetreulophidae based on next generation molecular data (Cruaud et al., submitted). Given the 9 antennal flagellomeres with a 1-segmented clava, strongly convex axillula, short frenum, and posteriorly displaced propodeal spiracle shared between *Omphalodipara* and other Hetreulophidae, it is reasonable to say that morphology agrees with this placement.

Heydeniidae new status, new placement

Heydenini Hedqvist, 1961. Type genus: *Heydenia* Förster, 1856. Spelling corrected to Heydeniini by Bouček (1988).

Diagnosis. Antenna with 10 or 11 flagellomeres, including 3 clavomeres. Eyes ventrally divergent. Clypeus without transverse subapical groove. Labrum exposed or hidden behind clypeus, sclerotized. Mandibles with 3 teeth. Pronotum expanded laterally and forming a subrectangular or laterally expanded structure from dorsal view (Fig. 67). Prepectus long, with large dorsal and ventral surfaces. Mesoscutellum either without a frenum, or with frenum laterally indicated by a frenal arm, with or without axillular sulcus (Fig. 68). Mesopleural area with acropleuron slightly expanded but occupying less than half its surface; mesepimeron not extending over anterior margin of metapleuron. All legs with 5 tarsomeres; profemur strongly (Fig. 69) or only mildly expanded; protibial spur stout and curved; basitarsal comb longitudinal. Metasoma with syntergum, therefore without epipygium, although terga not well-sclerotized and often difficult to assess.

Discussion. Some species of Heydeniidae are distinctive and resemble Ooderidae, while more generalized species are considerably more difficult to recognize. Ooderidae differ in having multiple rows of spine-like structures on the ventral surface of the always strongly expanded profemur. Heydeniidae have instead at most a single row of crest-like structures ventrally on the profemur. Otherwise, the ventrally elongate prepectus of Heydeniidae is distinctive. When the profemur is not strongly expanded and the pronotum is relatively short and not tent-like, species of *Heydenia* Förster can

be more difficult to recognize. Given the presence of a convex mesoscutellum with a weakly distinct or indistinct frenum and ventrally divergent eyes, generalized Heydeniidae may be confused with Cleonymidae or Lyciscidae, both of which have a much shorter prepectus ventrally.

Idioporidae new status

Idioporini LaSalle, Polaszek & Noyes, 1997. Type genus: *Idioporus* LaSalle & Polaszek, 1997.

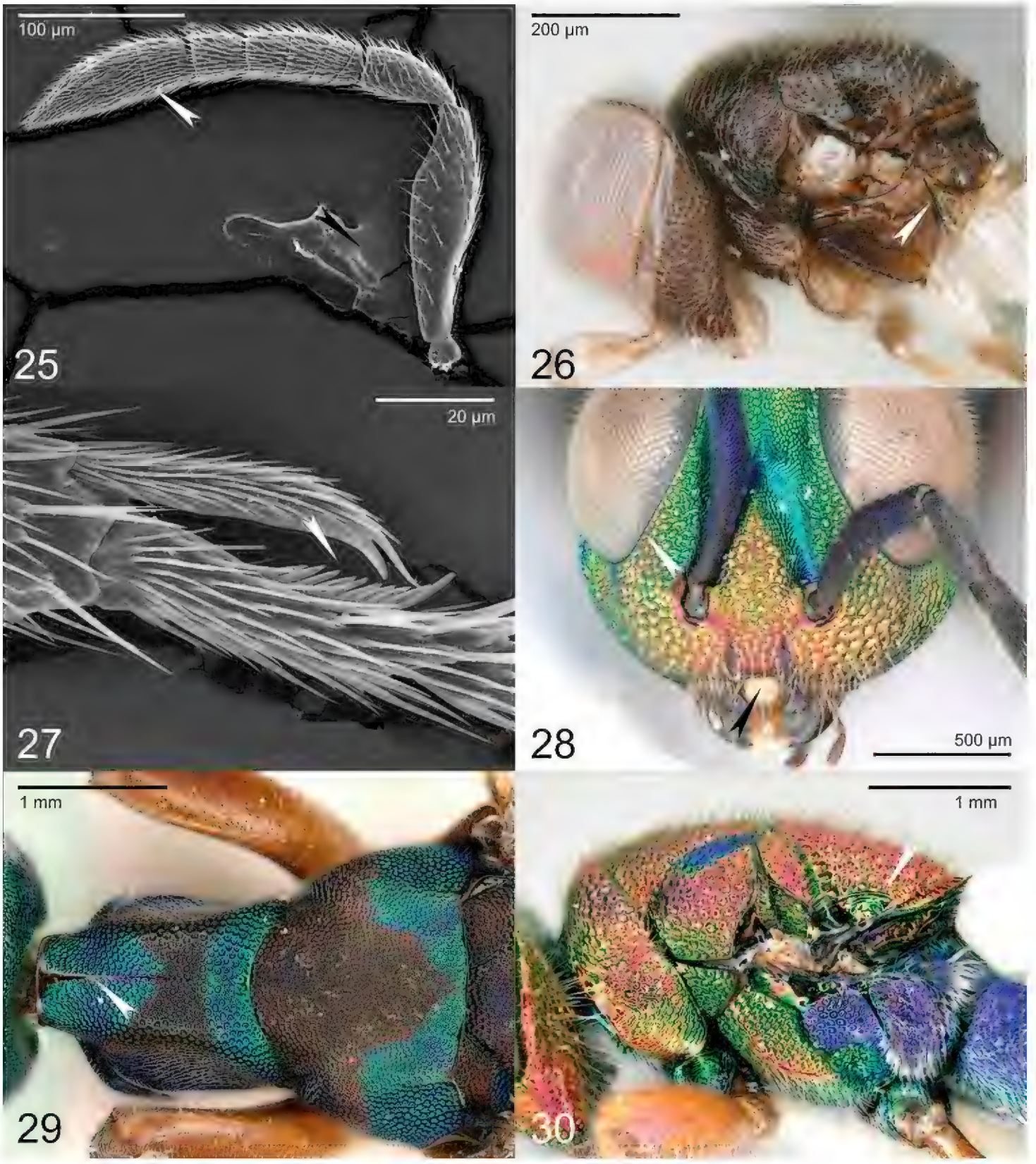
Diagnosis. Antenna with 9 flagellomeres, including 4 distinct clavomeres (Fig. 25). Clypeus with transverse subapical groove. Labrum hidden behind clypeus, flexible, subrectangular, with marginal setae in a row. Mandibles with 2 teeth. Subforaminal bridge with postgena separated by lower tentorial bridge. Mesopleural area without an expanded acropleuron; mesepimeron not extending over anterior margin of metapleuron (Fig. 26). All legs with 4 tarsomeres; protibial spur stout and slightly curved; basitarsal comb longitudinal (Fig. 27).

Discussion. *Idioporus affinis* LaSalle & Polaszek is a highly distinctive species in Chalcidoidea (LaSalle et al. 1997) that has been problematic in placement regardless of whether using morphology or molecules. Relative to most other families discussed here, it is distinct in tarsomere count; only *Zebe* La Salle (Pirenidae) has four tarsomeres, but *Zebe* differs in having most funiculars greatly reduced. *Idioporus* differs from other taxa with 4-segmented tarsi on all legs, such as Eulophidae and Calesidae, and in having a stout and slightly curved protibial spur.

Lyciscidae new status

Lyciscini Bouček, 1958. Type genus: *Lycisca* Spinola, 1840.

Diagnosis. Antenna with 8 or 7 flagellomeres, including usually a single clavomere but sometimes with 2 or (in males) 3 clavomeres. Eyes ventrally divergent (Fig. 28). Clypeus with or without transverse subapical groove. Labrum exposed or hidden behind clypeus, sclerotized and with a row of submarginal setae extending anteriorly (Fig. 28). Mandibles with 2 or 3 teeth, sometimes with a truncation in place of the dorsal teeth. Subforaminal bridge with elongate lower tentorial bridge and secondary tentorial pits that extend to the convergent hypostomal carina, with or without a postgenal groove and postgenal lamina, or (Solenurinae) with a postgenal bridge that externally separates the lower tentorial bridge from the convergent hypostomal carina. Pronotum with a smooth median longitudinal line or carina (Fig. 29). Notauli complete. Mesoscutellum usually without a frenum (Fig. 30) or (Solenurinae) with a frenum indicated by



Figures 25–30. 25–27 *Idioporus affinis* LaSalle & Polaszek (Idioporidae) **25** antenna **26** mesosoma lateral **27** protibial spur and basitarsal comb. **28** *Lycisca nebulipennis* Strand (Lyciscidae) head frontal view **29** *Lycisca ignicaudata* Westwood (Lyciscidae): pronotum and mesonotum dorsal view **30** *Agamerion cleptideum* (Westwood) (Lyciscidae): mesosoma lateral view.

lateral frenal arms (Fig. 32); without or (rarely) with axillular sulcus. Mesopleural area without an expanded acropleuron; mesepimeron not extending over anterior margin of metapleuron. All legs with 5 tarsomeres; protibial spur stout and curved; basitarsal comb longitudinal; metafemur with or without ventral teeth or expansion, with apical spurs arising from a truncate metatibial apex when the metafemur has ventral teeth.

Metasoma with syntergum, therefore without epipygium, although a complex set of carinae sometimes present on syntergum.

Discussion. The family Lyciscidae was potentially a major part of what Bouček (1988) had in mind when describing his concept of Cleonyminae as a monophyletic lineage, being "certainly one of the oldest in Pteromalidae, as seems to be supported by their association with wood-boring beetles." However, Lyciscidae itself appears to be relatively young and separate from Cleonymidae and all other members of the former sense of Cleonyminae, based upon next-generation molecular data (Cruaud et al., submitted).

Lyciscidae are relatively generalized and are therefore easily confused with many other large-bodied Chalcidoidea. While the longitudinal median smooth strip or carina of the pronotum is distinctive, it can be difficult to assess in some taxa depending on the position of the head. However, Neapterolelapinae differ from Lyciscidae chiefly in the lack of this feature. Many Eupelmidae are similar to Lyciscidae but females and some males have an expanded, convex and pad-like acropleuron that covers most or all of the mesopleural area. In all Chalcedectidae the metafemur has ventral teeth, a feature also present in some Lyciscidae, but in Lyciscidae the metatibia is truncate where the metatibial spurs insert, whereas in Chalcedectidae the spurs are either absent or placed on a ventroapical projection.

Lyciscidae differ from many other large-bodied Chalcidoidea in lacking a frenum. In Cleonymidae the notauli are incomplete. Pelecinellidae differ in having an elongate petiole with long setae perpendicular to its longitudinal axis. Macromesidae do not have ventrally divergent eyes, and often instead have ventrally convergent eyes. Eunotidae have a much shorter pronotum without a distinctive anterior neck.

For Solenurinae, identification can be more difficult due to the presence of a frenal arm, which is shared with a greater number of other chalcidoids. While *Solenura* Westwood itself is a highly distinctive genus with an elongate gaster, *Grooca* Sureshan & Narendran has a shorter gaster similar to that of many other Chalcidoidea. Confusion is most likely with other groups that have ventrally divergent eyes, such as Coelocybidae which differ in having strong setae on or nearly adjacent to the frenal groove. Herbertiidae and Micradelinae have a different antenna with 10 or 11 flagellomeres. Ditropinotellinae differ in having a distinctive T-shaped and elongate syntergum that resembles an elongate epipygium. Moranilidae may appear similar to Lyciscidae when comparing the lists of features, but in practice are easily distinguished. Some Moranilidae do not have ventrally divergent eyes (Asaphesinae), while others have a much smaller body with a different antennal flagellum that is strongly clavate and or with transverse funiculars.

Solenurinae Burks & Rasplus, new subfamily
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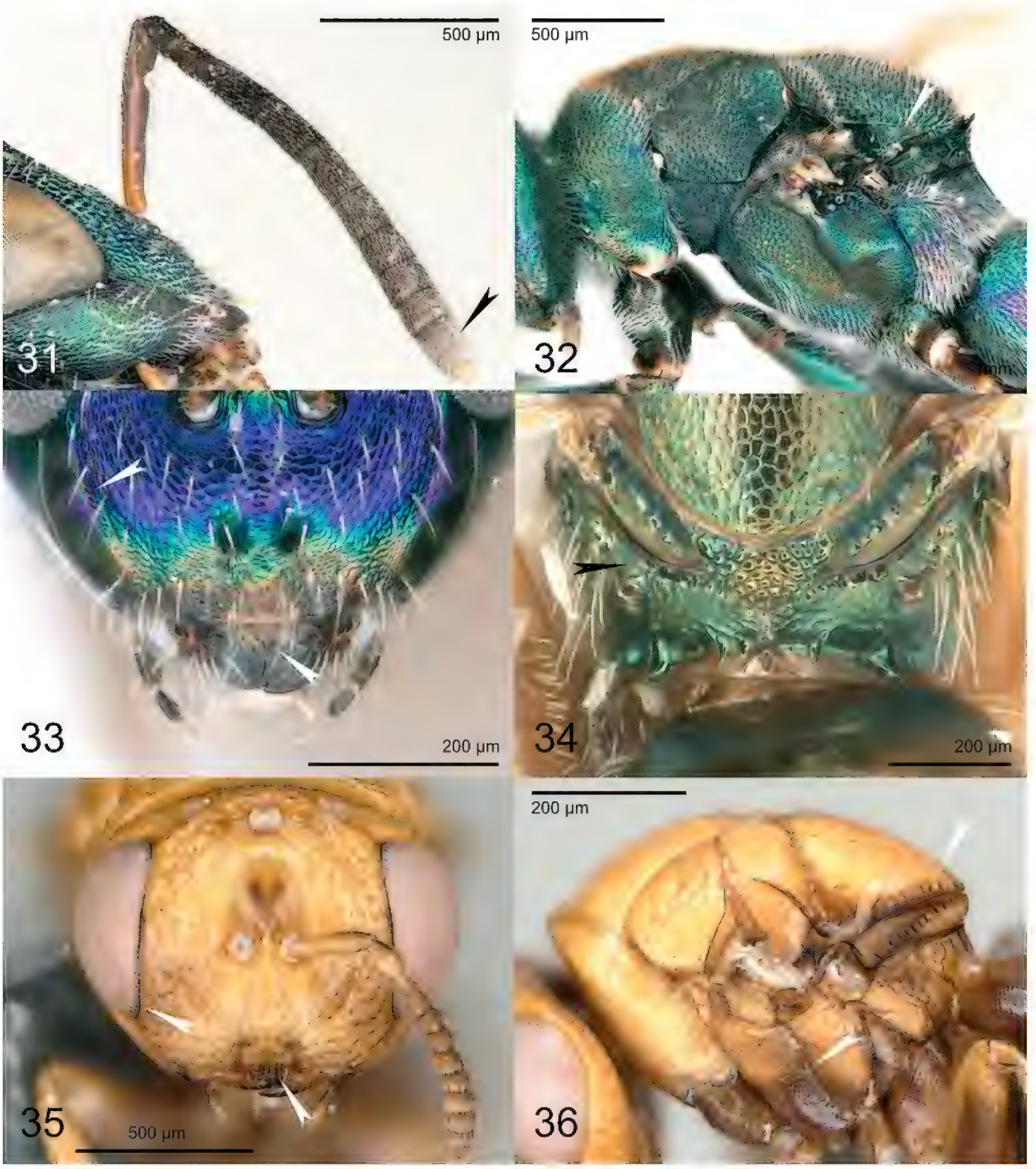
Type genus. *Solenura* Westwood, 1868.



Figures 31–36. 31, 32 *Solenura* sp. (Lyscicidae, Solenurinae) **31** antenna **32** mesosoma lateral **33** *Macromesus* sp. (Macromesidae): head frontal view **34** *Macromesus amphiretus* Walker (Macromesidae), propodeum **35, 36** *Trichilogaster acaciaelongifoliae* (Froggatt) (Melanosomellidae) **35** head frontal **36** mesosoma lateral view.

Diagnosis. Antenna with 2 or 3 clavomeres (Fig. 31). Clypeus without transverse subapical groove. Labrum exposed small and subrectangular, with marginal setae. Mandibles with 2 similarly-sized teeth. Subforaminal bridge with a postgenal bridge that externally separates the lower tentorial bridge from the convergent hypostomal carina; postgenal groove and postgenal lamina absent. Frenum indicated laterally by frenal arm that is well-separated from the marginal rim of the mesoscutellum (Fig. 32). Metafemur withoutventral teeth or expansion. Other features as in Lyciscinae.

Macromesidae new status

Macromesinae Graham, 1959. Type genus: *Macromesus* Walker, 1848.

Diagnosis. Antenna with 10 flagellomeres in females, 11 in males. Face between malar sulcus and torulus with a second longitudinal sulcus (Fig. 33). Clypeus without transverse subapical groove. Labrum subrectangular and hidden, with marginal setae in a row. Mandibles with 3 teeth (Fig. 33). Subforaminal bridge with postgena separated by lower tentorial bridge except for a small postgenal bridge dorsal to the hypostoma. Mesoscutellum with frenal arm indicated laterally, and with axillular carina or sulcus. Mesopleural area without an expanded acropleuron. Propodeum with spiracle separated by more than its own length from the anterior propodeal margin (Fig. 34). Fore and hind legs with 5 tarsomeres, middle legs in females with 4 tarsomeres. Protibial spur stout and curved; basitarsal comb longitudinal. Metasoma with syntergum, therefore without epipygium.

Discussion. *Macromesus*, the only genus of Macromesidae, differs from other Chalcidoidea inthe tarsomere count of females and the usually conspicuous second longitudinal sulcus on the lower face, although it otherwise bears some resemblance to other large-bodied chalcidoids with metallic coloration. The distance from the propodeal spiracle to the anterior margin of the propodeum may cause it to be confused with Ceidae or Hetreulophidae, but this feature is likely convergent, apparently occurring in Macromesidae because of its unusual propodeum.

Melanosomellidae new status

Melanosomellini Girault, 1913. Type genus: *Melanosomella* Girault, 1913.

Diagnosis. Antenna with 12 flagellomeres, including a small 4th clavomere. Eyes not divergent ventrally (Fig. 35). Clypeus without transverse subapical groove. Labrum hidden, flexible. Mandibles with 3 teeth. Subforaminal bridge with postgena separated by lower tentorial bridge, or with a short apparent postgenal bridge immediately dorsal to the hypostoma. Notauli complete. Mesoscutellum with frenum indicated laterally, either without axillular sulcus or carina, or with it greatly reduced and incomplete (Fig. 36). Mesopleural area without an expanded acropleuron (Fig. 36). All legs with 5 tarsomeres; protibial spur stout and curved; basitarsal comb longitudinal. Metasoma with syntergum, therefore without epipygium, and rigidly convex.

Discussion. Additionally, Melanosomellidae typically have a linear mesopleural sulcus that is more distinct than in most other Chalcidoidea (Fig. 36), although this feature also occurs in various species from other families. There is a strong chance of confusion of Melanosomellidae with Epichrysomallidae and Ormyridae, members of the Gall Clade (Cruaud et al., submitted, van Noort et al., in prep.). Epichrysomallidae are very similar to Melanosomellidae in habitus, but have different fore wing venation, with a nearly straight stigmal vein arising at a right angle from the wing

margin. Furthermore, Epichrysomallidae are strictly associated with *Ficus* (Moraceae) as gall-makers either within figs or on leaves and twigs. Ormyridae are also very similar to Melanosomellidae but have an occipital carina. Pteromalidae almost always have a distinct and complete axillular sulcus or carina. In species where this may not be the case, such as *Nikolskayana mirabilis* Bouček, the notauli are incomplete.

Encyrtocephalus Ashmead is very similar to other genera classified in Melanosomellidae, but molecular data (Cruaud et al., submitted) indicate that it may not belong inside this group. However, the only morphological features that imperfectly separate it from most Melanosomellidae are a large supracoxal flange on the posterior margin of the propodeum (Fig. 37) and a distinctly curved stigmal vein. These features are shared with a few other melanosomellid genera such as *Alyxiaphagus* Riek, with intermediates that would make diagnosis either very difficult or impossible. Therefore, *Encyrtocephalus* is kept in Melanosomellidae.

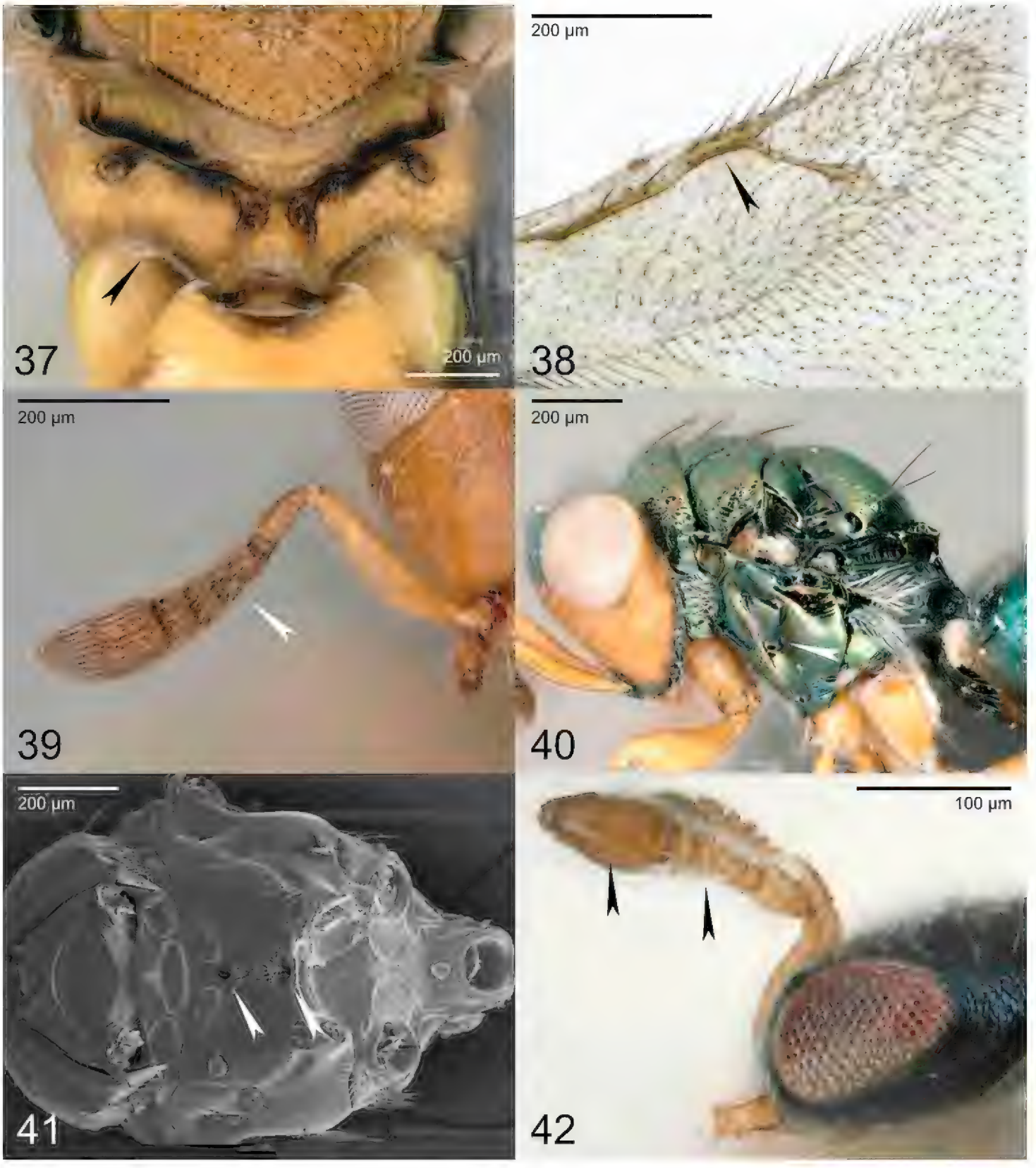
The fig associate species *Hansonita pertusae* Bouček new placement is transferred here because its fore wing venation resembles that of Melanosomellidae (Fig. 38) more strongly than that of Epichrysomallidae or other fig associates.

Moranilidae new status

Moranilini Bouček, 1988. Type genus: *Moranila* Cameron, 1883.
Tomocerodini Bouček, 1988. Type genus: *Tomocerodes* Girault, 1916.

Diagnosis. Antenna with 8 flagellomeres, clava undivided or incompletely divided (Fig. 39). Clypeus with transverse subapical groove (Fig. 56b). Labrum exposed, well-sclerotized, subrectangular with marginal setae in a row. Mandibles with 3 teeth. Subforaminal bridge with postgena separated by lower tentorial bridge. Mesoscutellum with frenum indicated at least laterally, with axillular sulcus. Mesopleural area without an expanded acropleuron, with pits (Fig. 40); mesepimeron not extending over anterior margin of metapleuron; two mesofurcal pits present (Fig. 41). All legs with 5 tarsomeres; protibial spur stout and curved; basitarsal comb oblique. Metasoma with syntergum, therefore without epipygium.

Discussion. Moranilidae contains two subfamilies: the former tribe Moranilinae new status and Tomocerodinae new placement, new status, based on morphological similarity since molecular data are absent for Tomocerodinae. Moranilidae differ from almost all other Chalcidoidea in having 2 mesofurcal pits instead of the usual single pit, but this feature appears to be homoplastic within Chalcidoidea. Indeed, some Eurytominae (Eurytomidae) (Krogmann and Vilhelmsen 2006) as well as Smicromorphinae and some Haltichellinae (G. Delvare comm. pers) also have two mesofurcal pits but differ from Moranilidae in many ways, including a different basitarsal comb and subforaminal bridge. These families are not easily confused with one another due to the very different habitus of the much more strongly sclerotized Eurytominae and Chalcididae.



Figures 37–42. 37 *Encyrtocephalus* sp. (Melanosomellidae): propodeum and supracoxal flange **38** *Hansonita pertusae* Bouček (Melanosomellidae): venation **39** *Moranila californica* (Howard) (Moranilidae): antenna **40** *Moranila viridivertex* (Girault) (Moranilidae): mesosoma lateral view **41** *Moranila californica* (Howard) (Moranilidae): mesosoma ventral view **42** *Neodipara masneri* Bouček (Neodiparidae): head lateral view and antenna.

Herbertiidae, Asaphesinae, and Enoggerinae new subfamily also share 2 mesofurcal pits with Moranilidae. Herbertiidae differ in lacking an axillular sulcus. Asaphesinae have 12 antennal flagellomeres instead of the maximum of 8 in Moranilidae. Enoggerinae lack a temple on the head, thus having the posterior margin of the eye coincident with that of the head dorsally. Micradelinae also resemble Moranilidae, but have only 1 mesofurcal pit instead of 2, and lack pits on the mesopleural area.

Tomocerodinae differ from Moranilinae in features discussed by Bouček (1988), most noticeably in the much shorter Gt_1, which is the longest tergum in Moranilinae but is much shorter than Gt_2 in *Tomocerodes*.

Neodiparidae new status

Neodiparini Bouček, 1961. Type genus: *Neodipara* Erdős, 1955.

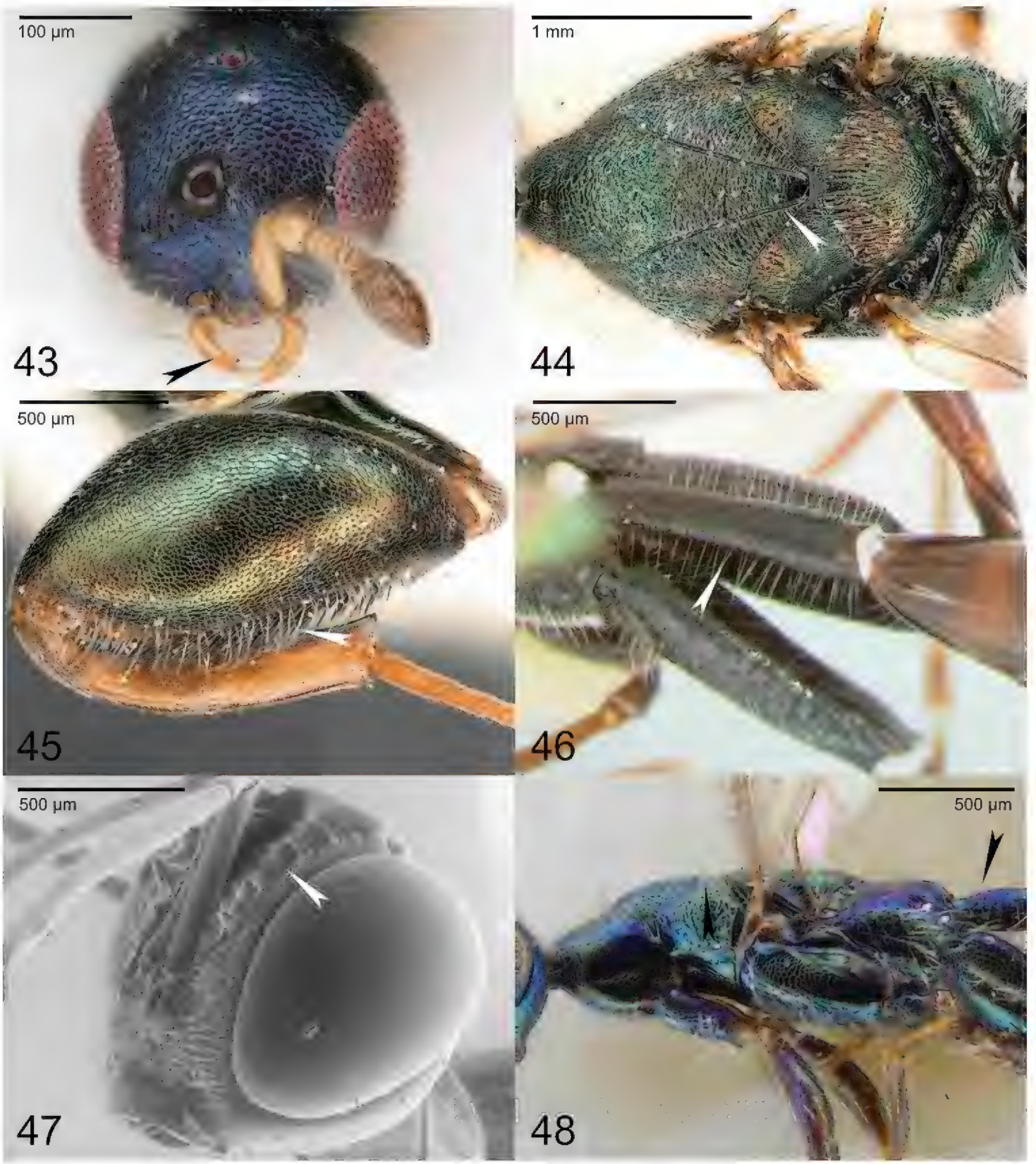
Diagnosis. Antenna with 10 (*Neodipara*) or 11 (*Elatoides*) flagellomeres, including 4 clavomeres (Fig. 42) and an inconspicuous anellus. Clypeus without transverse subapical groove. Labrum hidden, flexible, subcordiform with a median lobe, with marginal setae projecting forward from the lateral lobes (Fig. 43). Mandibles with 2 teeth (Neodiparinae) or with 2 teeth in the left mandible and 3 in the right (Elatoidinae). Subforaminal bridge with postgena separated by lower tentorial bridge. Mesoscutellum with frenum indicated at least laterally, without axillular sulcus. Mesopleural area without an expanded acropleuron; mesepimeron not extending over anterior margin of metapleuron. All legs with 5 tarsomeres; protibial spur stout and curved; basitarsal comb oblique. Metasoma with a separate epipygium.

Discussion. Although similar in habitus to some species with a long petiole from other families, such as Spalangiidae or some Pteromalidae, Neodiparidae differ from these in having a small separate epipygium instead of a syntergum, an oblique basitarsal comb, and a relatively large 4th clavomere. Elatoidinae new placement is transferred here, with its single genus *Elatoides* Nikol'skaya, differing from Neodiparinae in having a complete set of 11 flagellomeres instead of 10 and in the right mandible having 3 teeth.

Ooderidae new status

Ooderini Bouček, 1958. Type genus: *Oodera* Westwood, 1874.

Diagnosis. Antenna with 11 flagellomeres, including 3 clavomeres. Eyes ventrally divergent. Clypeus with transverse subapical groove. Labrum exposed, sclerotized. Mandibles with 2 or 3 weakly separated teeth or essentially truncate. Pronotum elongate, with lateral surfaces divergent such that the pronotum islaterally expanded (Fig. 44). Notauli complete, linear except for a short distance anteriorly, and almost meeting posteriorly, forming a distinctive 4-pronged pattern with the also sublinear part of the transscutal articulation that occurs along the anterior edge of the axilla (although this is often broken by a transverse fracture across the sulci) (Fig. 44). Mesoscutellum without a frenum but with an expanded posterior rim of the mesoscutellum that can resemble a frenum; without a distinct axillular sulcus but with some longitudinal sculpture in the axillular area. Mesopleural area without an expanded acropleuron; mesepimeron not extending over anterior margin of metapleuron. All legs with 5 tarsomeres; profemur expanded and with multiple rows of



Figures 43–48. 43 *Neodipara masneri* Bouček (Neodiparidae): head frontal view **44, 45** *Oodera formosa* Giraud (Ooderidae) **44** mesosoma dorsal view **45** fore leg **46** *Leptofoenus stephanoides* (Roman) (Pelecinellidae): petiole **47** *Doddifoenus rex* Bouček (Pelecinellidae): head antero-lateral view **48** *Nefoenus pilosus* Bouček (Pelecinellidae, Nefoeninae): mesosoma lateral view.

ventral spine-like structures (described in detail by Gibson 2003) (Fig. 45); protibial spur stout and curved; basitarsal comb longitudinal; metafemur not expanded and lacking ventral teeth. Metasoma with syntergum, therefore without epipygium.

Discussion. *Oodera* Westwood, the only genus in Ooderidae, is highly distinctive and does not resemble any other Chalcidoidea, especially in mesosomal features. The expanded profemur of *Oodera* can be compared with that of some Heydeniidae, which is also expanded but lacks the additional rows of spine-like structures of *Oodera*,

instead having broad ventral crest-like projections. Additionally, the laterally expanded pronotum also occurs in some Heydeniidae, which can have a somewhat comparable pattern of sulci on the mesoscutal dorsum, even though they are often less distinct in Heydeniidae. Otherwise, Pelecinellinae (Pelecinellidae) have parascrobal crests as in *Oodera*, although the two groups are differ in many other features.

Pelecinellidae new status

Pelecinellinae Ashmead, 1895. Type genus: *Pelecinella* Westwood, 1868.
Leptofoeninae Handlirsch, 1925. Type genus: *Leptofoenus* Smith, 1862.

Diagnosis. Antenna with 11 flagellomeres. Clypeus without transverse subapical groove. Mandibles with 3 teeth or with a broad apical truncation. Subforaminal bridge with postgenal bridge. Mesopleural area without an expanded acropleuron; mesepimeron extending over anterior margin of metapleuron. All legs with 5 tarsomeres; protibial spur stout and curved; basitarsal comb longitudinal. Petiole elongate with a row of lateral setae (Fig. 46).

Discussion. Leptofoeninae is here recognized as a junior synonym of Pelecinellidae, since Pelecinellinae (Ashmead 1895) was described earlier than Leptofoeninae (Handlirsch 1925) and because the situation does not qualify for preserving prevailing usage. Pelecinellidae are similar to other large-bodied chalcidoid parasitoids of wood-boring beetles, although they differ radically from all Chalcidoidea morphologically. Nefoeninae new placement is included here as a subfamily distinct from Pelecinellinae, on the strength of sharing the elongate petiole with lateral setae (Fig. 46) although it lacks the parascrobal crests present in Pelecinellinae (Fig. 47). An elongate petiole with lateral setae is unusual but not unique in Chalcidoidea, being present also in *Polstonia* Heydon (Pteromalidae: Miscogastrinae: Sphegigastrini), some *Spalangia* Latreille (Spalangiidae: Spalangiinae), and in some *Orasema* Cameron (Eucharitidae: Oraseminae) each of these differing greatly from Pelecinellidae in many other features. However, the form of the petiole in Nefoeninae (Fig. 48) is somewhat similar to that of Pelecinellinae, and the two groups share several other features, including elongation of the pronotum and certain other areas of the mesothoracic dorsum. While Ooderidae also have parascrobal crests, the pattern of sulci present on the mesothoracic dorsum in Ooderidae is unmistakable.

Pirenidae new status

Pireninae Haliday, 1844. Type genus: *Pirene* Haliday, 1833.
Tridyminae Thomson, 1876, new status. Type genus: *Tridymus* Ratzeburg, 1848.
Eriaporidae Ghesquière, 1955, new synonymy. Type genus: *Eriaporus* Waterston, 1917.
Eriaporinae Ghesquière, 1955, new status.
Euryischiinae Shaffee, 1974. Type genus: *Euryischia* Riley, 1889.
Cecidellinae new subfamily. Type genus: *Cecidellis* Hanson, 2005.

Diagnosis. Antenna with at most 11 flagellomeres, including 1 or more visible anellus, not counting any indistinct anelli that are usually present (Fig. 49). Eyes either not ventrally divergent, or diverging linearly (Cecidellinae, Eriaporinae, Euryischiinae), instead of with a concave medial margin in their lower half as in Cleonyminae and others (the exceptions are some male *Macroglenes* Westwood with huge eyes). Clypeus without transverse subapical groove. Labrum hidden, flexible, subrectangular with marginal setae in a row. Mandibles with 3 or 4 teeth, splayed in a characteristic way (Bouček 1988) (Fig. 50). Subforaminal bridge with postgena separated by lower tentorial bridge. Notauli complete. Mesoscutellum with frenum indicated at least laterally, and with axillular sulcus. Mesopleural area without an expanded acropleuron; mesepimeron not extending over anterior margin of metapleuron. All legs with 5 tarsomeres, except in *Zebe* La Salle with 4; protibial spur stout and curved; basitarsal comb longitudinal. Metasoma with syntergum, therefore without epipygium.

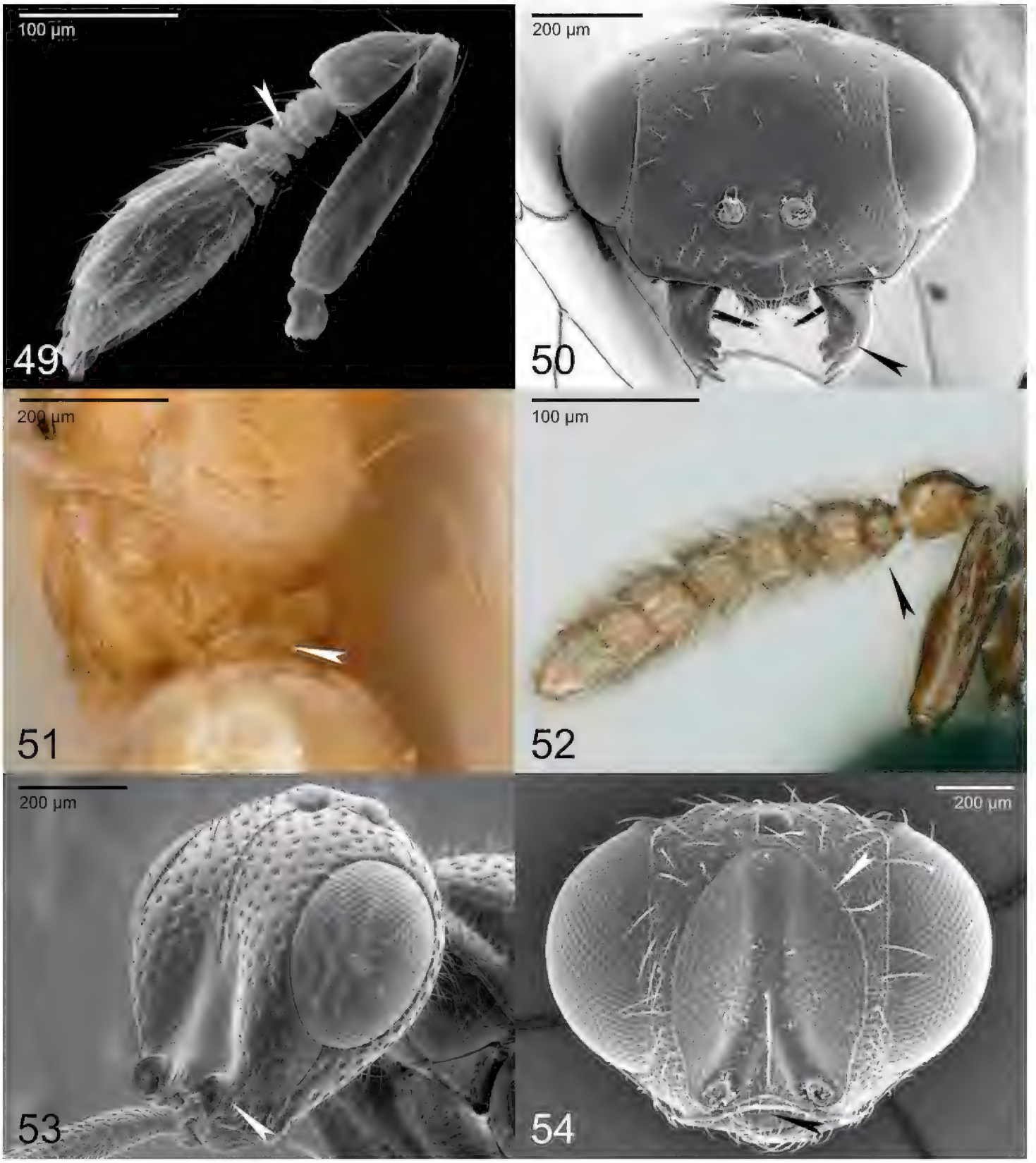
Discussion. The family Eriaporidae is synonymized with Pirenidae, with Eriaporinae and Euryischiinae retained as separate subfamilies. Cecidellinae is described for the unusual genus *Cecidellis*.

Pirenidae most strongly resemble those few Pteromalidae that have 11 antennal flagellomeres, otherwise differing from most in having 5 funiculars or fewer, without enough visible anelli to bring the total flagellomeres before the clava to the count of 8 that is present in nearly all Pteromalidae. Out of those Pteromalidae with 11 flagellomeres, *Termolampa pinicola* Bouček differs in having incomplete notauli, *Andersena anomala* Andersen differs in having no anelli. *Bugacia* Erdős differs in having the vertex with blunt carina or crest, and *Trigonoderopsis* Girault differs in having 8 flagellomeres between pedicel and clava. Eunotidae differ in having an exposed, rigid labrum and divergent eyes with a concave medial margin in their lower half. While this may make Eunotidae and Pirenidae sound very similar to one another, the habitus of Eunotidae is very different from most Pirenidae, being stout and flattened instead of being more moderate in body proportions and with a deeper mesosoma. Eriaporinae are the pirenids most likely to be confused with Eunotidae, but differ most conspicuously in having stout setae on the parastigma. Moranilidae differ in having 2 mesofurcal pits, in having pits on the mesopleural area of the mesopectus, and in having an oblique basitarsal comb. Herbertiidae and Systasidae differ from Pirenidae in having 2 mandibular teeth, and along with Micradelinae, an exposed, rigidly sclerotized labrum.

Cecidellinae Mitroiu, Rasplus & Burks, new subfamily
https://zoobank.org/4295BD83-C89D-403E-9BFC-260C63134ADF

Type genus. *Cecidellis* Hanson, 2005.

Diagnosis. Body pale, white to yellowish or pale brown, without metallic luster. Antenna with 9 flagellomeres, including 4 funiculars and 2 anelli. Eyes linearly diverging in ventral half. Petiole with lamina that overlaps part of the propodeal margin (Heydon and Hanson 2005) (Fig. 51). Otherwise as in Pirenidae.



Figures 49–54. 49 *Macroglenes varicornis* (Haliday) (Pirenidae): antenna **50** *Gastrancistrus* sp. (Pirenidae, Tridyminae): head frontal view **51** *Cecidellis* sp. (Pirenidae, Cecidellinae): petiole with lamina **52** *Spathopus* sp. (Pirenidae, Tridyminae): antenna **53** *Spalangia alycia* Gibson (Spalangiidae): head anterolateral view **54** *Erotolepsia* sp. (Spalangiidae, Erotolepsiinae): head frontal view.

Pireninae

Diagnosis. Body usually dark brownish or metallic. Antenna with at most 3 large flagellomeres and at least 2 anelli before clava (Fig. 49). Eyes usually not or only slightly diverging ventrally (except some males). Marginal vein at least 3.5× as long as the short and mostly straight stigmal vein. Petiole without dorsal lamina.

Discussion. In this new, more restricted sense, Pireninae contains genera that are morphologically similar to *Macroglenes*. They are here distinguished from Tridyminae, which are generally more stout in body shape and differ in features mentioned in diagnoses of both subfamilies, but most prominently in the antennal flagellum and relative lengths of the marginal and stigmal veins of the fore wing.

Tridyminae revived status

Tridymina Thomson, 1876. Type genus: *Tridymus* Ratzeburg, 1848. Treated as Tridyminae by Ashmead (1904).

Diagnosis. Body usually metallic, except *Calyconotiscus* Narendran & Saleem. Antenna with 4 or 5 large flagellomeres and at least one anelliform flagellomere before clava (Fig. 52). Eyes not divergent ventrally. Marginal vein at most 3× as long as the relatively long stigmal vein. Petiole without dorsal lamina.

Discussion. The subfamily Tridyminae is removed from synonymy with Pireninae to include *Gastrancistrus* Westwood new placement and related genera. *Calyconotiscus* Narendran & Saleem new placement, *Ecrizotes* Förster new placement, *Epiterobia* Girault new placement, *Melancistrus* Graham new placement, *Oxyglypta* Förster new placement, *Premiscogaster* Girault new placement, *Sirovena* Bouček new placement, *Spathopus* Ashmead new placement, and *Spinancistrus* Kamijo new placement are here confirmed to belong to this subfamily.

Spalangiidae revived status

Spalangiidae (as Spalangiae, not Latin) Haliday, 1833, revived status. Type genus: *Spalangia* Latreille, 1805.
Erotolepsiinae Bouček, 1988. Type genus: *Erotolepsia* Howard, 1894.

Diagnosis. Antenna usually with 8 flagellomeres, including a 1-segmented clava, with 11 flagellomeres including 3 clavomeres in *Eunotopsia* Bouček. Clypeus without transverse subapical groove. Labrum exposed, well-sclerotized, subrectangular or semicircular with marginal setae in a row (Fig. 53). Mandibles with 2 or 3 teeth, or undivided (in *Eunotopsia*). Subforaminal bridge with postgenal bridge or with postgena separated by lower tentorial bridge. Mesoscutellum with frenum indicated at least laterally, and without axillular sulcus. Mesopleural area without an expanded acropleuron; mesepimeron extending over anterior margin of metapleuron. All legs with 5 tarsomeres; protibial spur stout and curved; basitarsal comb longitudinal. Metasoma with syntergum, therefore without epipygium.

Discussion. There are two distinctive subfamilies in Spalangiidae, Spalangiinae and Erotolepsiinae new placement, both comprised of parasitoids of Diptera. The antennal

toruli are placed very low on the head in most species of both subfamilies (Fig. 54). In most Erotolepsiinae (except *Eunotopsia* where they are placed higher), the toruli are just above the very short clypeus, while in Spalangiinae the toruli are placed on lobes that overhang the clypeus and labrum, rendering them difficult to see. This distinctive antennal placement and the prognathous head make members of Spalangiinae easily identifiable. Most Erotolepsiinae (again, not *Eunotopsia*) are readily identified by the presence of a long carina that encircles most of the face, extending from near the median ocellus to the top of the clypeus (Fig. 54), and have a transverse carina across the anterior part of Gt_1 (Fig. 55). The enigmatic genus *Eunotopsia* shares the transverse carina on Gt_1 with other Erotolepsiinae and can be identified to subfamily using this feature. Erotolepsiinae strongly resemble Herbertiidae and Micradelinae, which differ in lacking the carinae of the face and Gt_1. Herbertiidae further differ in having an oblique basitarsal comb, although the basitarsal comb of Micradelinae is reduced and difficult to evaluate. Eunotidae are also somewhat similar to Erotolepsiinae, but differ in that the mesepimeron does not overlap the anterior margin of the metapleuron, and in lacking the Gt_1 sculpture of Erotolepsiinae.

Systasidae new status

Systasini Bouček, 1988, new status. Type genus: *Systasis* Walker, 1834.
Trisecodinae new subfamily. Type genus: *Trisecodes* Delvare & LaSalle, 2000.

Diagnosis. Antenna with 7 or 11 flagellomeres, including 1 or more anellus and a small 4th clavomere. Eyes not ventrally divergent. Clypeus without transverse subapical groove. Labrum exposed, well-sclerotized (Fig. 56a). Subforaminal bridge with postgena separated by lower tentorial bridge. Notauli complete. Mesoscutellum with short frenum indicated at least laterally, with axillular sulcus. Mesopleural area without an expanded acropleuron; mesepimeron not extending over anterior margin of metapleuron; mesofurcal pit on mesotrochantinal plate directly between the mesocoxal insertions (Fig. 57). Protibial spur curved; basitarsal comb oblique; all legs with either 5 (Systasinae) or 3 (Trisecodinae) tarsomeres. Metasoma with syntergum, therefore without epipygium.

Discussion. Systasinae are most likely to be confused with Pirenidae and Pteromalidae, which differ in having a flexible labrum that is concealed behind the protruding clypeus, whereas the clypeus in Systasinae recedes medially to expose the sclerotized labrum; they also have a longitudinal basitarsal comb, whereas it is oblique in Systasinae. The position of the mesofurcal pit in Systasidae is very unusual, although a leg may need to be removed to see it. Trisecodinae can be confused with Trichogrammatidae based on the 3-segmented tarsi, the head sulci, and the setal lines on the fore wing, and with some Eulophidae, based on the reduced number of flagellomeres, the head sulci, the setal lines on the fore wing, and the very short postmarginal and stigmal veins. From the former, Trisecodinae differ in the longer flagellum, the narrowly attached gaster with phragma

restricted to mesosoma, the different pattern of head sulci, and the shape of the fore tibial spur. From the latter, although *Trisecodes* was preliminary placed in Entedoninae (Delvare & LaSalle, 2000), Trisecodinae differ in various features that do not fit with any current eulophid subfamily. While *Trisecodes* is easy to distinguish from other Systasidae due to the difference in tarsomere count, it is retained in this family to indicate the phylogenetic context provided by both the molecular and morphological data.

Trisecodinae Mitroiu, Rasplus & Burks, new subfamily

https://zoobank.org/C3DBCDA4-F0C1-4E89-AC82-5BCDC745147D

Type genus. *Trisecodes* Delvare & LaSalle, 2000.

Diagnosis. Antenna with 7 flagellomeres (Fig. 58); multiporous plate sensilla unusually long and curved; head except malar sulcus with frontal, scrobal and subtorular sulci; anterior tentorial pits absent; toruli at or below the lower ocular line; all legs with 3 tarsomeres.

Former Pteromalidae taxa treated as *incertae sedis* in Chalcidoidea, unplaced to family

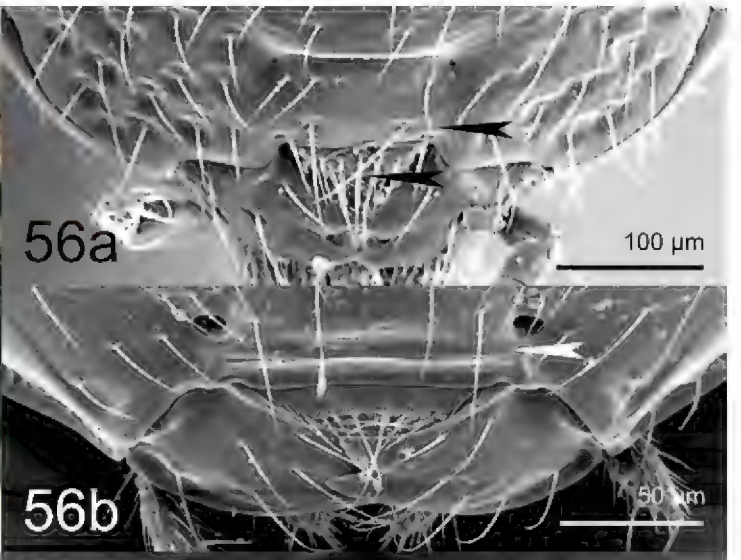
Asaphesinae *incertae sedis* new placement

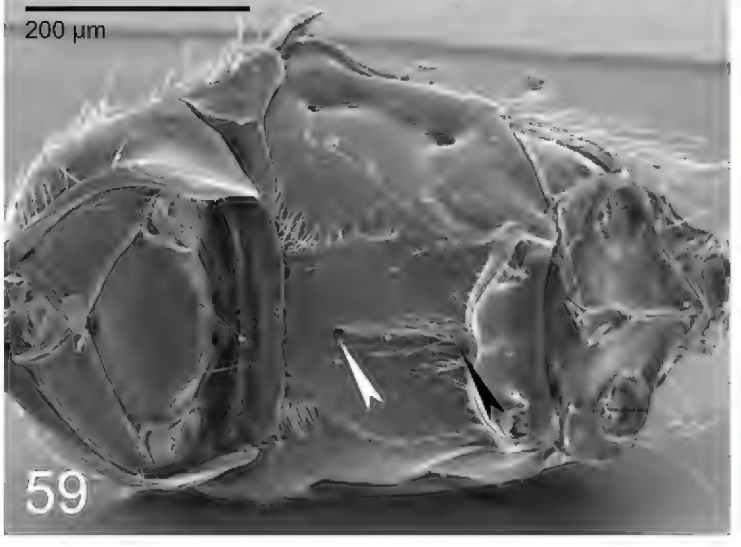
Asaphinae Ashmead, 1904. Type genus: *Asaphes* Walker, 1834. Junior homonym of Asaphidae Burmeister, 1843.

Asaphesinae Burks & Heraty, 2020, replacement name.

Diagnosis. Antenna with 12 flagellomeres, including a small 4th clavomere. Clypeus with transverse subapical groove. Head dorsally with temple separating posterior margin of eye from that of the head. Labrum exposed, well-sclerotized, subrectangular with marginal setae in a row. Mandibles with 2 or 3 teeth. Subforaminal bridge with postgena separated by lower tentorial bridge; occipital carina present. Mesoscutellum with frenum indicated at least laterally, and with axillular sulcus. Mesopleural area without an expanded acropleuron, with pits; mesepimeron not extending over anterior margin of metapleuron; two mesofurcal pits usually present (Fig. 59) (absent in the fossil genus *Coriotela*). All legs with 5 tarsomeres; protibial spur stout and curved; basitarsal comb oblique. Metasoma with syntergum, therefore without epipygium.

Discussion. The scope of Asaphesinae is much reduced with the removal of Enoggerinae new subfamily to a separate *incertae sedis* subfamily in Chalcidoidea, and *Bairamlia* Waterston to Sphegigastrini (Pteromalidae). Asaphesinae is part of a set of taxa with two mesofurcal pits and some other shared features, but which do not form a clade in molecular analyses (Cruaud et al, submitted), including Enoggerinae, Herbertiidae, and Moranilidae. Asaphesinae differ from Herbertiidae and Moranilidae in having 12 flagellomeres instead of a maximum of 10. Enoggerinae differ in lacking a temple, thus with the posterior margin





Figures 55–60. 55 *Erotolepsia* sp. (Spalangiidae, Erotolepsiinae): mesosoma and base of metasoma dorsal view **56a, 57** *Systasis* sp. (Systasidae) **56a** apex of clypeus without subapical groove **57** mesosoma ventral, mesotrochantinal plate and mesofurcal pit **58** *Trisecodes africanum* Gumovsky (Pirenidae, Trisecodinae): antenna **56b, 59** *Asaphes* sp. (Asaphesinae, *incertae sedis*) **56b** clypeal subapical groove **59** mesosoma ventral **60** *Austrosystasis atricorpus* Girault (Austrosystasinae, *incertae sedis*) **60** head frontal view, mesosoma lateral view.

of the eye dorsally meeting that of the head. Some Asaphesinae resemble Pteromalidae in habitus, differing in the clypeus, reduced mandibles, labrum, oblique basitarsal comb, and presence of two mesofurcal pits, but also having features that are rarely found in Pteromalidae, such as an occipital carina and the mesopleural area with pits.

Austrosystasinae *incertae sedis* new placement

Austrosystasinae Bouček, 1988. Type genus: *Austrosystasis* Girault, 1924.

Diagnosis. Antenna with 12 flagellomeres, including a small 4th clavomere. Eyes slightly linearly divergent ventrally. Clypeus with transverse subapical groove. Labrum hidden, flexible, with marginal setae in a row (Fig. 60). Subforaminal bridge with postgena separated by lower tentorial bridge, with a short apparent postgenal bridge immediately dorsal to the hypostoma. Mesoscutellum with frenum indicated laterally, with axillular sulcus. Mesopleural area without an expanded acropleuron; mesepimeron not extending over anterior margin of metapleuron (Fig. 61). All legs with 5 tarsomeres; protibial spur stout and curved; basitarsal comb longitudinal. Metasoma with syntergum, therefore without epipygium, rigidly convex.

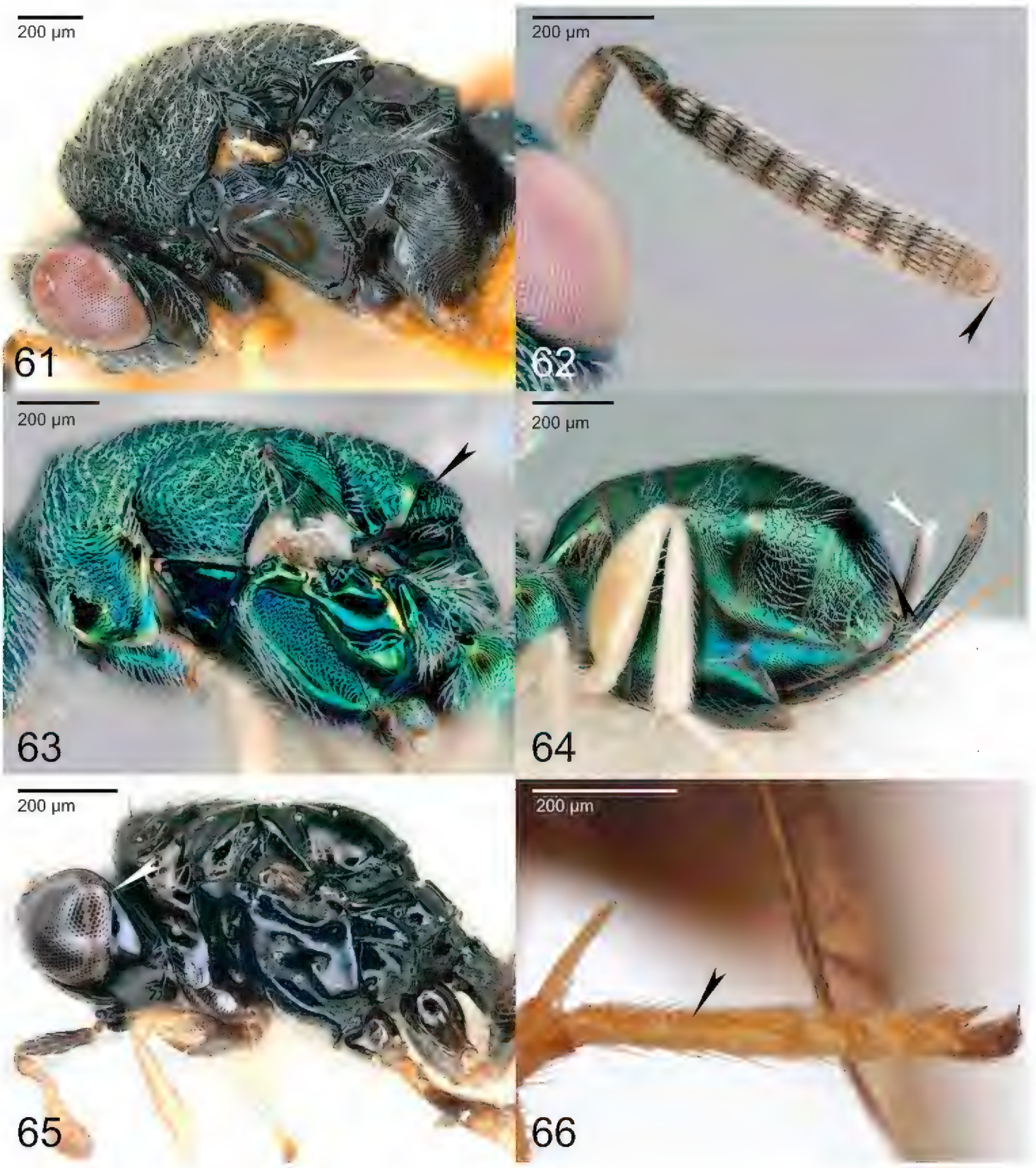
Discussion. *Austrosystasis atricorpus* Girault, the sole species in this subfamily, has not been sequenced, and its place is uncertain given our incomplete knowledge of its morphology. It appears to be a member of the Gall Clade, and it is an associate of galls on *Elaeocarpus* (Elaeocarpaceae) in Australia. It has rough surface sculpture (Fig. 61) that causes it to resemble Eurytomidae (especially Rileyinae), although it has a shorter pronotum. Otherwise, it resembles Melanosomellidae, differing in having a distinct and complete axillular sulcus and distinctive sculpture on the axillula. It also resembles Ormyridae in overall body shape, but this could be attributed to gall association in both taxa. The differing sculpture of the axillula and the posterior surface of the head separate Austrosystasinae from Ormyridae. Given that *A. atricorpus* would complicate the diagnosis of whatever family it could be transferred to, the genus is dealt with here as *incertae sedis* in Chalcidoidea.

Ditropinotellinae *incertae sedis* new placement

Ditropinotellinae Bouček, 1988. Type genus: *Ditropinotella* Girault, 1915.

Diagnosis. Antenna with 11 flagellomeres, without a 4th clavomere (Fig. 62). Eyes slightly divergent ventrally. Clypeus without a transverse subapical groove, with a small median incision. Labrum hidden behind clypeus, flexible. Mandibles with 3 teeth. Occipital carina absent. Subforaminal bridge with a postgenal bridge. Notauli complete. Mesoscutellum with a densely setose frenum that is indicated laterally, without axillular sulcus (Fig. 63). Mesopleural area without an expanded acropleuron; mesepimeron not extending over anterior margin of metapleuron. All legs with 5 tarsomeres; protibial spur stout and curved; basitarsal comb longitudinal. Metasoma with an elongate, T-shaped syntergum in females that may resemble an epipygium because of its shape (Fig. 64).

Discussion. *Ditropinotella* Girault is a morphologically enigmatic Australasian genus of gall associates, transferred out of Torymidae and placed in its own subfamily in



Figures 61–66. 61 *Austrosystasis atricorpus* Girault (Austrosystasinae, *incertae sedis*): mesosoma lateral view **62–64** *Ditropinotella* sp. (Ditropinotellinae, *incertae sedis*) **62** antenna **63** mesosoma lateral view **64** metasoma **65** *Enoggera reticulata* Naumann (Enoggerinae, *incertae sedis*): mesosoma lateral view **66** *Eopelma* sp. (*incertae sedis*): apex of mesotibia and mesotarsus.

Pteromalidae by Bouček (1988). It renders Eupelmidae paraphyletic in next-generation molecular data (Cruaud et al., submitted), although it lacks the expanded acropleuron of that family and lacks the diagnostic features of all genera in Calosotinae. *Ditropinotella* has a broad membranous area posterior to its mesocoxae, although this also occurs in various other chalcidoids that are not related to Eupelmidae. The possibility remains that *Ditropinotella* may be a reduced eupelmid, but morphological

evidence in support of this possibility is lacking. Because of the possible instability of this situation, Ditropinotellinae is removed from Pteromalidae to be treated as *incertae sedis* in Chalcidoidea.

The general habitus, setose frenum, and approximated, slightly advanced axilla of *Ditropinotella* invite comparison with Torymidae, which differ in having a true epipygium in females that is shorter and not so elongate. Males are more difficult to distinguish, differing in the slightly divergent eyes and incised clypeus of *Ditropinotella*, features that do not occur together in Torymidae. Most Megastigmidae also resemble *Ditropinotella*, although most Megastigmidae and Torymidae have an occipital carina. Megastigminae additionally differ from Ditropinotellinae in having an enlarged fore wing stigma and along with Chromeurytominae have a true epipygium in females, while Keiraninae have an occipital carina and do not have an elongate syntergum. Although some pteromalid fig associates have an elongate epipygium that resembles the syntergum of *Ditropinotella*, these differ from *Ditropinotella* in having a larger axillula with a distinct axillular sulcus. Male Eupelminae can strongly resemble those of *Ditropinotella*, but differ in having a distinct frenal arm laterally.

Enoggerinae Burks, new subfamily, *incertae sedis*
https://zoobank.org/BB289EAC-0821-480F-9E60-B4E75358AE4F

Type genus. *Enoggera* Girault, 1926.

Diagnosis. Antenna with 9–12 flagellomeres, including either an incompletely divided clava or up to 4 clavomeres, sometimes including a small 4th clavomere. Temple absent, thus posterior margin of eye coincident with the posterior margin of the head dorsally (Fig. 65). Clypeus with transverse subapical groove. Labrum exposed, well-sclerotized, subrectangular, with marginal setae in a row. Mandibles with 3 teeth. Subforaminal bridge with postgena separated by lower tentorial bridge. Mesoscutellum with frenum indicated at least laterally, with axillular sulcus. Mesopleural area without an expanded acropleuron, with pits; mesepimeron not extending over anterior margin of metapleuron; two mesofurcal pits present. All legs with 5 tarsomeres; protibial spur stout and curved; basitarsal comb oblique. Metasoma with syntergum, therefore without epipygium. Egg parasitoids of Chrysomelidae (Coleoptera).

Discussion. Enoggerinae share a pair of mesofurcal pits with a number of other chalcidoid groups, including Herbertiidae, Moranilidae, and Asaphesinae. However, these groups are unstable in molecular analyses and do not form a clade (Cruaud et al., submitted), with Enoggerinae more often as the sister group of Coelocybidae. Therefore, Enoggerinae can be separated from all similar groups by the absence of the temple. With a different biology, Enoggerinae would also represent a discordant element if placed in any of the other groups.

Eopelma Gibson *incertae sedis* new placement

Eopelma Gibson, 1989. Type species. *Eopelma mystax* Gibson, 1989.

Diagnosis. Antenna with 8 flagellomeres, with an undivided clava. Eyes ventrally divergent. Clypeus without transverse subapical groove. Labrum hidden behind clypeus, flexible. Mandibles with 3 teeth or with a ventral tooth and dorsal slightly emarginate truncation. Axilla long, separated anteromedially. Axillular sulcus more or less distinct. Frenum absent. Acropleuron enlarged, convex and pad-like; covering most of mesopleural area, separated from mesocoxa by the lower mesepimeron, metapleuron, and a dorsal extension of the metasternal area. All legs with 5 tarsomeres; protibial spur stout and curved; basitarsal comb longitudinal; ventral membranous area anterior to mesocoxal attachment lacking; mesotibial spur stout; mesotarsus with 1 row of pegs anteroventrally (Fig. 66). Metasoma with syntergum, therefore without epipygium.

Discussion. *Eopelma* is consistently the sister group of another *incertae sedis* taxon, *Storeya* Bouček (Storeyinae), in next-generation molecular analysis (Cruaud et al., submitted). These two groups do not strongly resemble each other in body shape. *Storeya* does not have an expanded acropleuron, and has not previously been indicated as a relative of any eupelmid. They do share an antennal flagellomere count, a long radicle, general coloration, and an undivided clava, but the list of shared features possessed by these two genera is much shorter than the list of differences between them. A new subfamily is not described for *Eopelma* because it is a single genus, the position of which in Chalcidoidea is still in question.

Eopelma vaguely resembles *Neanastatus* Girault in body shape and coloration. *Neanastatus* differs in having a much smaller axilla, which may not be clearly visible.

Keryinae *incertae sedis* new status, new placement

Keryini Bouček, 1988. Type genus: *Kerya* Bouček, 1988.

Diagnosis. Antenna with 10 flagellomeres, including a single anellus (Fig. 70). Clypeus with lateral sulci but without a dorsal sulcus; ventral margin protruding and slightly convex but not bilobed (Fig. 70). Toruli slightly above center of face, immediately below a forked sulcus that exposes conjunctiva. Trabeculae absent (although sulcus present in middle of upper face). Notauli complete, incised. Frenum present, indicated by a complete frenal sulcus (Fig. 71). Axillular sulcus present. Acropleuron not enlarged (Fig. 71). Fore wing densely setose, without speculum; basal fold pigmented. Legs with 4 tarsomeres on all legs; protibial spur short and straight. Cerci surrounded by conjunctiva.

Discussion. The combination of having just 4 tarsomeres on all legs, 10 flagellomeres, and a frenum, together with a lack of trabeculae, makes *Kerya antennalis* Bouček distinct from all other chalcidoids. It was once placed in Eulophinae (Bouček 1988),

Figures 67–72. 67–69 *Heydenia longicollis* (Cameron) (Heydeniidae) **67** mesosoma dorsal view **68** mesosoma lateral view **69** fore leg **70, 71** *Kerya antennalis* Bouček (Keryinae, *incertae sedis*) **70** head frontal view and antenna **71** mesosoma lateral view **72** *Callimomoides* sp. (Louriciinae, *incertae sedis*): head frontal view.

although analysis of 28S D2 ribosomal DNA indicated that it is not a eulophid and it was moved to Ormocerinae based on the placement of the toruli and the arched body (Gauthier, et al. 2000). Indeed some Melanosomellidae resemble *K. antennalis* in body shape, color, and smooth surface sculpture, but they have 11 or more flagellomeres, a bilobed clypeal margin, 5 tarsomeres, a stout and curved protibial spur, cerci surrounded

by cuticle, no axillular sulcus, and no forked sulcus on the face. Eulophidae and some Aphelinidae also have 4 tarsomeres and are relatively generalized (unlike Calesidae and Idioporidae), but have fewer flagellomeres and no frenum. Given the strong differences between *K. antennalis* and all the taxa with which it has been previously placed, and because it has not been analyzed using next-generation molecular data, Keryini is here elevated to subfamily status and placed as *incertae sedis* in Chalcidoidea.

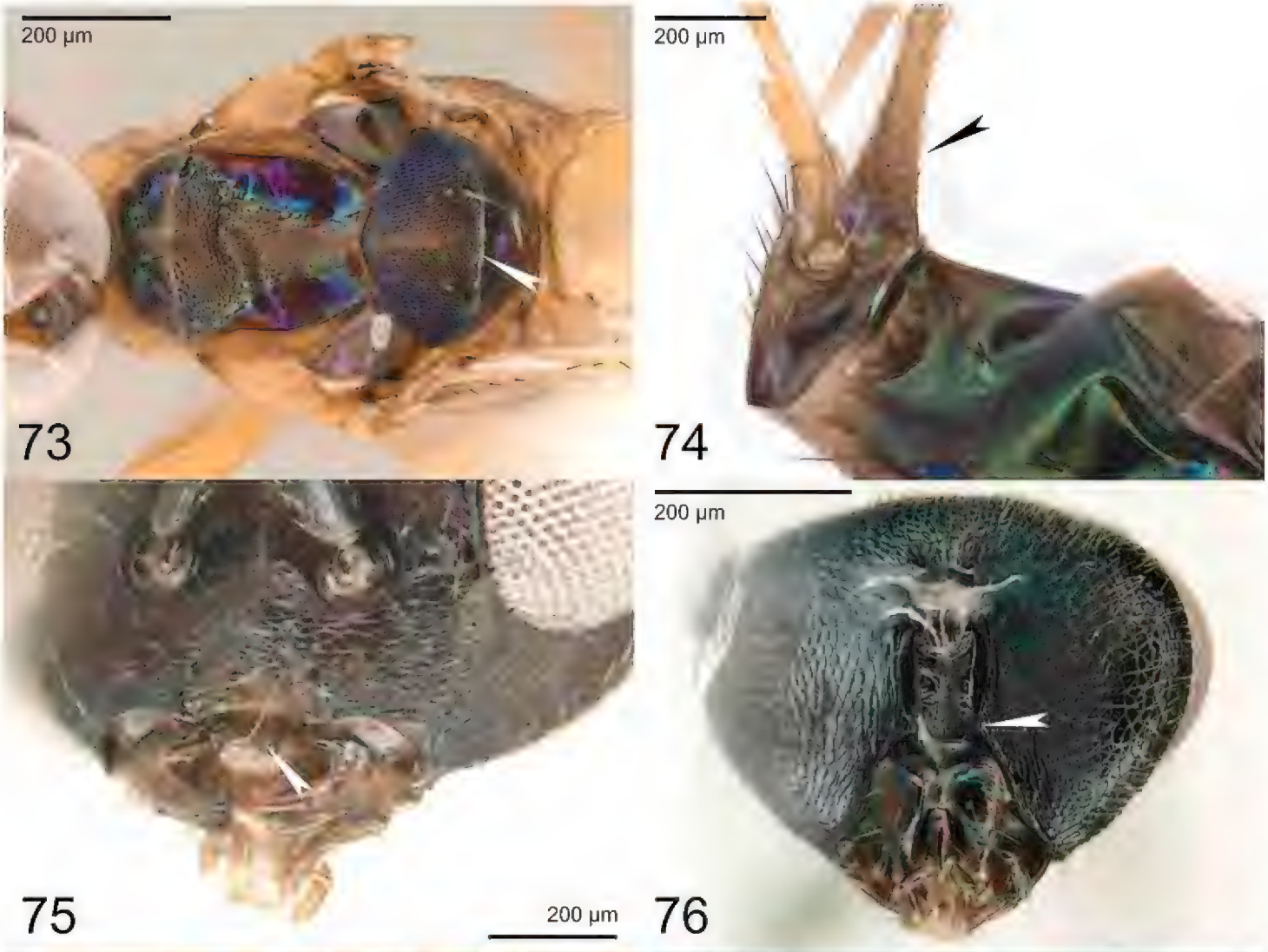
Louriciinae *incertae sedis* new placement

Louriciini Hedqvist, 1961: 92,108. Type genus: *Louricia* Ferrière, 1936. Treated as Louriciinae by Bouček (1988).

Diagnosis. Antenna with 8 flagellomeres, including an undivided clava and 2 anelli; radicle elongate. Eyes ventrally divergent. Face with a network of grooves that is usually concealed by the strongly collapsing head (Fig. 72). Clypeus without transverse subapical groove. Labrum subrectangular and exposed, with marginal setae in a row. Mandibles with 3 teeth. Subforaminal bridge with a postgenal bridge separating the secondary tentorial pits from the hypostoma. Pronotum long, with a slightly expanded lateral surface and therefore somewhat expanded laterally. Notauli complete, linear and incised. Axilla strongly advanced (Fig. 73). Mesoscutellum with frenum indicated at least laterally or by an abrupt transition to smooth surface sculpture, without axillular sulcus (Fig. 73). Mesopleural area without an expanded acropleuron. All legs with 5 tarsomeres; protibial spur stout and curved; basitarsal comb longitudinal. Metasoma in females with elongate syntergum extending over the exserted ovipositor (Fig. 74).

Discussion. Next-generation molecular analysis (Cruaud et al., submitted) consistently recovers the distinctive *Callimomoides* Girault as a member of a strongly supported clade that also includes *Neanastatus* and *Lambdobregma*, with *Callimomoides* as the sister group of *Neanastatus*, which therefore renders Neanastatidae paraphyletic. Morphologically, this relationship is highly debatable and no unique character supports it. However, this strong morphological disparity may be due to difference in life history as *Callimomoides* is an egg parasitoid of Cerambycidae while *Neanastatus* is parasitic in galls of Cecidomyiidae (Diptera) and *Lambdobregma* could be parasitoids of cricket eggs (Gibson 1989). While *Callimomoides* has an enlarged mesotibial spur and a large membranous area posterior to the mesocoxa, these features are not conclusive proof of relationship with Neanastatidae because they are found in various other taxa as well. There are no diagnostic features shared with either *Neanastatus* or *Lambdobregma*.

The highly unusual gestalt of *Callimomoides*, together with the combination of linear notauli, long pronotum, and stout mesotibial spur, prevent it from being easily confused with other Chalcidoidea. Eulophidae can have similar notauli and a weakly sclerotized, collapsing head and body, but differ in having 4 tarsomeres on all legs.



Figures 73–78. 73, 74 *Callimomoides* sp. (Louriciinae, *incertae sedis*) **73** mesosoma dorsal view **74** extremity of metasoma, elongated syntergum **75, 76** *Micradelus acutus* Graham (Micradelinae, *incertae sedis*) **75** head frontal view **76** head posterior view **77** *Neapterolaelaps* sp. (Neapterolelapsinae, *incertae sedis*): antenna **78** *Pseudoceraphron albifrons* (Bouček) (Neapterolelapsinae, *incertae sedis*): head posterior view.

Micradelinae *incertae sedis* new placement

Micradelini Wall, 1972. Type genus: *Micradelus* Walker, 1834. Treated as Micradelinae by Vago (2006).

Diagnosis. Antenna with 10 or 11 flagellomeres, including 3 or 4 clavomeres. Eyes slightly ventrally divergent. Clypeus transverse, with transverse subapical groove. Labrum exposed,

well-sclerotized, subrectangular with marginal setae in a row (Fig. 75). Mandibles with 2 teeth or with a small 3rd dorsal tooth (Fig. 75). Subforaminal bridge with postgena separated by lower tentorial bridge except for a small postgenal bridge dorsal to the hypostoma; posterior surface of head without (Fig. 76) postgenal lamina or postgenal groove. Pronotum transverse in dorsal view. Mesoscutellum with frenum reduced, with frenal arm laterally but sometimes hardly separated from marginal rim of mesoscutellum; axillular sulcus present. Mesopleural area without expanded acropleuron, without pits; mesepimeron extending over anterior margin of metapleuron; one mesofurcal pit present. Fore wing marginal vein subequal to stigmal vein in length; uncus elongate. All legs with 5 tarsomeres; protibial spur stout and curved. Metasoma with syntergum, therefore without epipygium.

Discussion. The former tribe Micradelini was treated as a subfamily by Vago (2006) and we preserve that rank here, although we remove it from Pteromalidae based on both molecular and morphological data (Cruaud et al., submitted). While Micradelinae are very similar to Herbertiidae in body shape, they only occasionally form a monophyletic group and Micradelinae are particularly unstable in phylogenetic placement.

Morphologically, Micradelinae strongly resemble Herbertiidae and the *incertae sedis* genus *Rivasia* Askew & Nieves-Aldrey in habitus and other features. The basitarsal comb of *Micradelus* Walker is reduced and difficult to evaluate, although it may be oblique like that of Herbertiidae. Herbertiidae differ from Micradelinae in having a much shorter stigmal vein relative to the marginal vein, in lacking an axillular sulcus, in lacking the postgenal groove and postgenal sulcus on the back of the head, and in having 2 mesofurcal pits instead of the single pit of Micradelinae. *Rivasia* is very similar to Micradelinae in most features, differing in having a more elongate body including the pronotum, and in having metallic green coloration instead of the short, stout body and brownish coloration of Micradelinae. Eunotidae may appear similar to Micradelidae when comparing lists of features, but in practice are easily distinguished in their different habitus and in having a short fore wing uncus.

Neapterolelapinae Rasplus, Burks & Mitroiu, new subfamily *incertae sedis* new placement

https://zoobank.org/802C4B39-1937-4EE0-B153-25861437F3DB

Type genus. *Neapterolelaps* Girault, 1913.

Diagnosis. Antenna with 11 flagellomeres, with 3 clavomeres (Fig. 77). Eyes ventrally divergent. Clypeus with a transverse subapical groove. Labrum exposed, sclerotized, subtriangular with setae. Mandibles with 2 or 3 narrow teeth. Subforaminal bridge with elongate lower tentorial bridge and secondary tentorial pits that extend to the convergent hypostomal carina, with or without a postgenal groove and postgenal lamina (Fig. 78). Pronotum without a smooth median longitudinal line or carina. Mesoscutellum without frenum, at least sometimes with a small axillula indicated by an axillular sulcus or carina. Mesopleural area without an expanded acropleuron; mesepimeron not extending over anterior margin of metapleuron. All legs with 5 tarsomeres; protibial spur stout and curved; basitarsal comb longitudinal; metafemur without ventral teeth or expansion. Metasoma with syntergum, therefore without epipygium; cercal brush present.

Discussion. *Neapterolelaps* and *Pseudoceraphron* Dodd form the sister group of Lyciscidae in next-generation molecular data, although they were previously classified in Diparinae (Bouček 1988; Desjardins 2007; Desjardins et al. 2007). While Desjardins (2004) mentioned the name Neapterolelapini in his doctoral dissertation, it was not mentioned in the two resulting publications. Additionally, it was mentioned by Heraty et al. (2013), although it was not diagnosed in that publication and therefore was not described there. Janšta (2014) also mentioned Neapterolelapini in a doctoral dissertation, but did not diagnose it. None of these previous usages satisfy article 13.1.1 of the ICZN Code, and therefore Neapterolelapinae is described as new here and it is removed from Diparidae to be treated as *incertae sedis* in Chalcidoidea. *Nosodipara* Bouček is also placed here based on morphology.

Given the characters described here, confusion with Lyciscidae is most likely, which differ in having a longitudinal median pronotal carina. However, a lack of metallic coloration on the mesosoma (but sometimes not of the head) of females makes Neapterolelapinae much more likely to be confused with Diparidae, which contains numerous species that resemble this group. Diparidae differ in having a conspicuous frenum in most species, although this may be indistinct or absent in highly derived brachypterous species. These must be distinguished using features of the head, such as the hidden labrum, convex clypeal margin, absence of clypeal subapical groove (excepted in *Dipara*) and striation of metacoxa of Diparidae versus the exposed labrum, concave clypeal margin, presence of clypeal subapical groove and absence of striation on metacoxa in Neapterolelapinae.

The placement of Neapterolelapinae does not conflict with the findings of Desjardins et al. (2007), who also placed *Neapterolelaps* as the sister group of what is now Lyciscidae in molecular analyses. This placement was discussed as "difficulty in uniting" [Diparinae] by Desjardins (2007).

Parasaphodinae *incertae sedis* new placement

Parasaphodinae Bouček, 1988c: 345. Type genus: *Parasaphodes* Schulz, 1906.

Diagnosis. Antenna with 11 flagellomeres, including 1 anellus and 7 funiculars (Fig. 79a). Eyes ventrally not or slightly divergent. Clypeus without transverse subapical groove. Labrum hidden (Fig. 80). Mandibles with 2 teeth. Mesoscutellum with frenum not distinctly indicated, without axillular sulcus. Mesopleural area without an expanded acropleuron, without pits; mesepimeron with posterior margin deeply concave and extending over anterior margin of metapleuron. All legs with 5 tarsomeres; protibial spur stout and curved. Marginal and postmarginal veins widened adjacent to stigmal vein (Fig. 79b).

Discussion. No molecular data are available for Parasaphodinae; moreover, because of the poor preservation of most available specimens, several characters such as the basitarsal comb, the structure of the back of the head, or the mesofurcal pits could not be observed. It is thus very difficult to assess the taxonomic position of Parasaphodinae in relation to other chalcids, therefore we treat it as *incertae sedis* in Chalcidoidea. Similarities with Asaphesinae, Elatoidinae and Herbertiidae have been discussed (Mitroiu 2017), but all these groups differ from Parasaphodinae in many respects.

Rivasia Askew & Nieves-Aldrey *incertae sedis* new placement

Rivasia Askew & Nieves-Aldrey, 2005. Type species: *Rivasia fumariae* Askew & Nieves-Aldrey, 2005

Diagnosis. Antenna with 8 flagellomeres, including an undivided or incompletely divided clava. Eyes slightly ventrally divergent. Clypeus transverse. Labrum exposed, well-sclerotized. Mandibles with 2 teeth. Subforaminal bridge with postgena separated by lower tentorial bridge except for a small postgenal bridge dorsal to the hypostoma; posterior surface of head without postgenal lamina or postgenal groove. Pronotum subconical and elongate in dorsal view. Mesoscutellum with frenum; mesopleural area without an expanded acropleuron, without pits; mesepimeron extending over anterior margin of metapleuron; one mesofurcal pit present. Fore wing marginal vein subequal to stigmal vein in length; uncus elongate. All legs with 5 tarsomeres; protibial spur stout and curved. Metasoma with syntergum, therefore without epipygium.

Discussion. *Rivasia* is usually the sister group of fellow *incertae sedis* taxon Asaphesinae in molecular analyses (Cruaud et al., submitted), although the two groups share few distinctive features morphologically. Instead, *Rivasia* more strongly resembles the subfamily Micradelinae, though never forming a clade with it. *Rivasia* shares no particularly distinctive features with Ormocerinae (Pteromalidae) nor any former part of it, differing from them in numerous features listed in the diagnosis.

Micradelinae can be distinguished from *Rivasia* by having a shorter, transverse pronotum and brownish coloration, in contrast with the longer pronotum and metallic coloration of *Rivasia*. Asaphesinae differ from *Rivasia* in a number of features, including the presence of 8 flagellomeres instead of 12, the lack of an occipital carina, and from extant species in the lack of pits on the mesopleural area.

Storeyinae *incertae sedis* new placement

Storeyinae Bouček, 1988. Type genus: *Storeya* Bouček, 1988.

Diagnosis. Antenna with 8 flagellomeres, including an undivided clava; radicle elongate (Fig. 81). Intertorular prominence absent (Fig. 81). Eyes slightly divergent ventrally. Clypeus without transverse subapical groove. Labrum hidden behind clypeus, flexible, subrectangular and with marginal setae in a row. Mandibles with 3 teeth (may be 2 in some specimens in which it is difficult to see). Subforaminal bridge with a postgena separated by lower tentorial bridge. Notauli incomplete. Mesoscutellum with frenum indicated; with axillular sulcus. Mesopleural area without an expanded acropleuron; mesepimeron extending over anterior margin of metapleuron. Fore wing with a tuft of thickened leaf-shaped setae on the parastigma (Fig. 82). All legs with 5 tarsomeres; protibial spur stout and curved; basitarsal comb longitudinal. Metasoma with syntergum, therefore without epipygium.

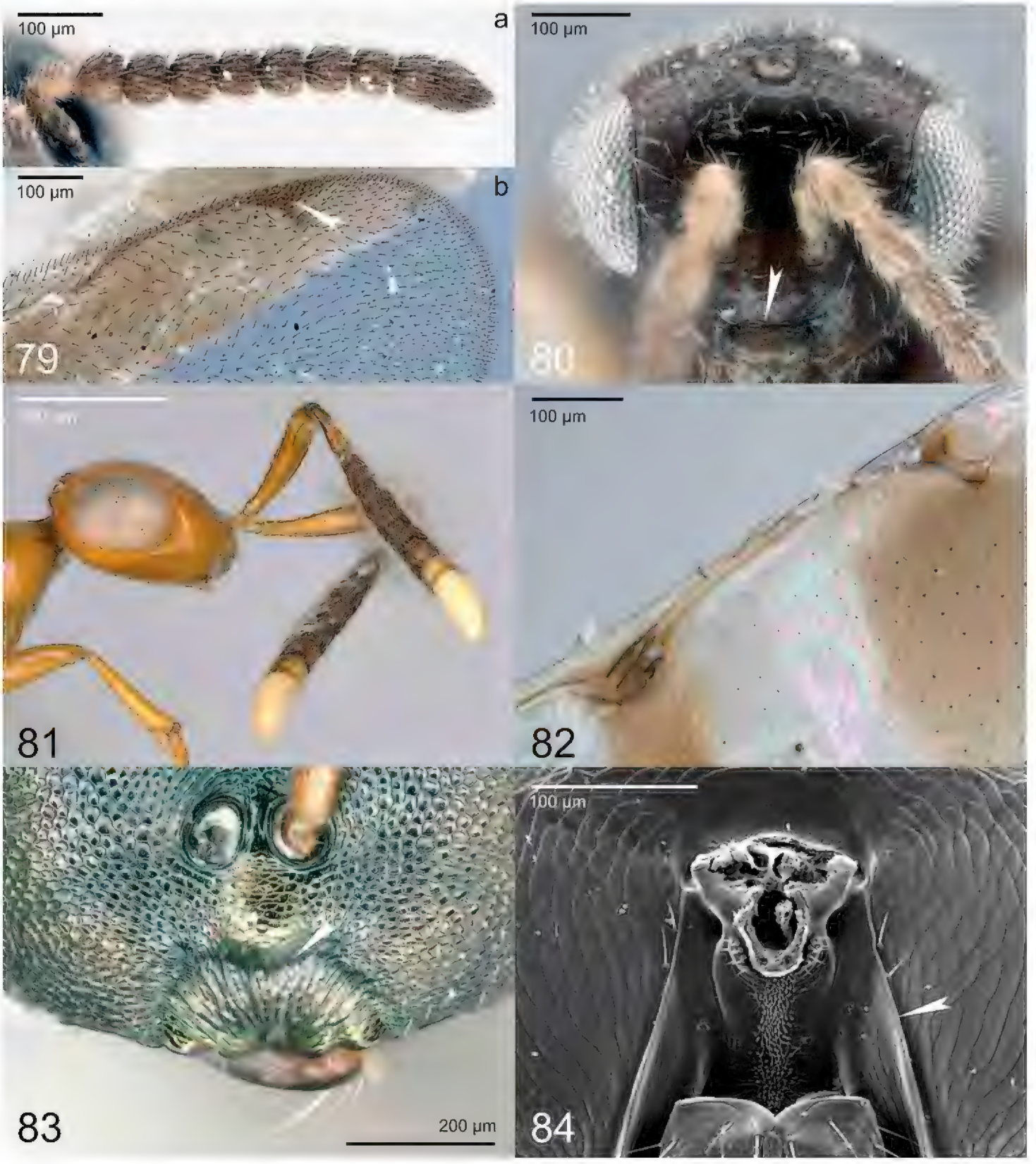
Discussion. Molecular and morphological data do not provide a clear signal on where this subfamily should be placed, and therefore we treat it as *incertae sedis* in Chalcidoidea. The elongate antennal radicle is an unusual feature also shared by its sister group (*Eopelma*) in molecular analyses and, in comparable taxa, is only found in Louriciinae. The enlarged axillula, easily visible dorsally, invites comparison with Colotrechninae and Sycophaginae in Pteromalidae, and with Hetreulophidae, although each of these groups differs from Storeyinae in having complete notauli and in many other features as well. The low placement of the toruli may cause Storeyinae to key near Spalangiinae in family keys, although the toruli are not on lobes and the two groups differ in many features. The body coloration (excepted for one undescribed iridescent species) and the tuft of thickened, leaf-shaped setae on the parastigma recall Cerocephalidae, although Storeyinae lack an intertorular prominence and are not placed with cerocephalids using molecular data.

Pteromalidae

Pteromalini Dalman, 1820. Type genus: *Pteromalus* Swederus, 1795. Treated as Pteromalidae by Walker (1834).

Diagnosis. Antenna with 12 flagellomeres in nearly all cases (except in some fig associates, *Amphidocius*, *Andersena anomala*, *Bugacia*, *Trigonoderopsis*, and possibly *Termolampa pinicola*), including a small 4th clavomere; with at least 5 funiculars, and if with 5 then with 2 or more anelli. Eyes not ventrally divergent (although some genera have modified eyes that are difficult to evaluate). Clypeus subquadrate and without ventral transverse groove (Fig. 83). Labrum flexible (Darling 1988) and hidden behind clypeus. Mandibles with 3 or 4 teeth each (except in some fig associates (1–3 teeth) and in *Austroterobia* Girault where the left mandible has 2 teeth but is falcate). Subforaminal bridge with postgena separated by lower tentorial bridge; posterior surface of the head without postgenal lamina or postgenal groove (Fig. 84). Mesoscutellum with frenum indicated at least laterally, with axillular sulcus (except in some fig associates and *Nikolskayana mirabilis*). Mesopleural area without an enlarged acropleuron. All legs with 5 tarsomeres; protibial spur stout and curved; basitarsal comb longitudinal. Gaster, while sometimes rigidly convex, not strongly sclerotized; metasomal apex in most species with a syntergum and therefore without an epipygium (except in some fig associates).

Discussion. Agaonidae are similar to fig-associated Pteromalidae, differing from all in having a mandibular appendage bearing rows of spurs or lamellae in females (*Seres* Waterston, which may appear especially similar to Agaonidae, have an enlarged plate-like mandible, see figs 14–16 in van Noort and van Arten 2006, but do not have a mandibular appendage), and in more or less fused anelli, the last one mostly spine-like (Fig. 85). Male Agaonidae differ from male pteromalid fig wasps in that the metasomal apex is telescoped in a U-shaped arrangement under the body. Eucharitidae differ from most Pteromalidae in that the pronotum is not visible from dorsal view, but also in the flattened marginally digitate labrum. Likewise, most of the members of the Planidial Clade (Zhang et al. 2022) such as Chrysolampidae (digits sometimes ab-



Figures 79–84. 79 *Parasaphodes afer* Mitroiu (Parasaphodinae, *incertae sedis*) **79 a** antenna **b** venation **80** *P. iceryae* (Ashmead) (Parasaphodinae): head frontal view **81, 82** *Storeyia* sp. (Storeyinae, *incertae sedis*) **81** head lateral view and antenna **82** venation **83** *Caenocrepis* sp. (Pteromalidae, Pteromalinae): lower face **84** *Nasonia vitripennis* (Walker) (Pteromalinae): head dorsal view.

sent in Chrysolampinae and labrum plate-like in Philomidinae), Eutrichosomatidae, and Perilampidae have a digitate labrum. Eulophidae differ in having 4-segmented tarsi and a short, straight protibial spur. Some Eurytomidae, such as Rileyinae and *Buresium* Bouček can be similar to a few Pteromalidae, even though nearly all Pteromalidae have a much smaller pronotum; in a few cases where the pronotum is long, e.g. Trigonoderinae, it is not subrectangular in dorsal view, but instead is gradually narrowing anteriorly. Rileyinae and *Buresium* differ from Pteromalidae in having a

postgenal groove and a strongly sclerotized gaster. In practice, Rileyinae and *Buresium* are easily recognized once they are familiar, and no Pteromalidae have the combination of a long pronotum with a rigidly convex gaster. Ormyridae also differ from Pteromalidae in having a carapace-like gaster. Other members of the Gall Clade, such as Epichrysomallidae and Melanosomellidae, can be very similar to those pteromalids with complete notauli, but they differ in having either no indication of an axillular sulcus or carina, or in having a reduced and incomplete one. Pirenidae differ in having fewer flagellomeres: most especially if they have 5 funiculars, then they only have 1 anellus. Torymidae and Megastigmidae differ from most Pteromalidae in having an epipygium in females (except in *Keirana* Bouček which has a transverse sulcus across its syntergum immediately anterior to the cerci), but some pteromalid fig associates have a separate epipygium and a long, exserted ovipositor, therefore strongly resembling both of these families. Torymidae differ from all Pteromalidae in the form of their postgenal bridge, which occurs in the form of postgenal lobes meeting each other over the hypostoma (Burks and Heraty 2015). Most fig-associated Pteromalidae have the postgena separated by the lower tentorial bridge (Rasplus et al. 1998), additionally differing in ways described by Grissell (1995). Those with an elongate head, such as *Sycoecus* Waterston, have rederived a true postgenal bridge but differ from Torymidae in the shape of the highly modified head itself and in the vast number of other unusual features of their highly modified bodies.

From the new families diagnosed above, Pteromalidae can be distinguished using the given diagnoses. Species with 2 mandibular teeth differ in this count from nearly all Pteromalidae except for in the left mandible of *Austroterobia*, but in *Austroterobia* the mandibles are additionally very different in that they are falcate, whereas the bidentate mandibles of other families, such as Ceidae, are small and narrow. A partial exception to this is Neodiparidae, where the mandibles are relatively large but still not the same shape as in *Austroterobia* and are not falcate.

Yusufia Koçak & Kemal and *Ksenoplata* Bouček are kept as unplaced to subfamily in Pteromalidae new placement, because of uncertainty over their molecular placement and difficulty in assigning them to a subfamily morphologically. They would render any other subfamily more difficult to diagnose, although they bear some similarity to Miscogastrinae and Trigonoderinae in having a clypeal margin with a single median tooth.

Subfamilies and tribes of Pteromalidae

Colotrechninae

Colotrechnides Thomson, 1876. Type genus: *Colotrechnus* Thomson, 1878. Treated as Colotrechninae by Ashmead (1899).

Diagnosis. Mandibles not falcate. Scapula not exposed anteriorly by pronotum. Axilla strongly advanced (Fig. 86). Axillula enlarged and convex (Fig. 86). Propodeum with or without plicae. Petiole simple, usually transverse and hardly visible.

Amerostenini

Amerostenini Bouček, 1988. Type genus: *Amerostenus* Girault, 1913.

Diagnosis. Antennal flagellum with 4 anelli and 4 funiculars (Fig. 87). Pronotum not medially divided. Ovipositor sheaths not expanded.

Discussion. Molecular data indicate that the previously mentioned (Bouček 1988) unusual morphology of *Yrka dahmsi* Bouček new placement suggests that it belongs in the tribe Amerostenini in Colotrechninae instead of in Coelocybidae.

Morphology is consistent with this change, given that *Yrka* and some Amerostenini share a count of 4 antennal anelli.

Colotrechnini

Uzkini Bouček, 1988. Type genus: *Uzka* Bouček, 1988.

Diagnosis. Antennal flagellum usually with 3 anelli and 5 funiculars, but sometimes with 2 anelli and 6 funiculars. Pronotum not medially divided. Ovipositor sheaths not expanded.

Discussion. Uzkini new syn. is treated as a synonym of Colotrechnini due to the lack of distinguishing features between them. *Uzka* Bouček has not been analyzed molecularly, but morphologically it is distinguished by a differently shaped head, and therefore seems to be a derived element within Colotrechnini instead of being part of a distinct lineage.

Divnini

Divnini Bouček, 1988. Type genus: *Divna* Bouček, 1988.

Diagnosis. Antennal flagellum with 2 anelli and 5 funiculars. Pronotum medially divided (Fig. 88). Ovipositor sheaths expanded and densely setose.

Discussion. The sole species in Divnini, *Divna hirtura* Bouček, has not been analyzed molecularly, and has only a dubious membership in Colotrechninae or even in Pteromalidae. Divnini is retained in Colotrechninae because we are not aware of any definitive reason to remove it from Pteromalidae, but molecular data or new morphological data may well suggest a change in its placement.

Trigonoderopsini Rasplus & Mitroiu, new tribe

https://zoobank.org/00E4A87B-E416-4B34-8156-0EAD9B597BC3

Type genus. *Trigonoderopsis* Girault, 1915.

Diagnosis. Antenna variously with 11 flagellomeres, either with 1 anellus and 5 funiculars, 2 anelli and 5 funiculars, 1 anellus and 6 funiculars, or with 1 anellus and

7 funiculars in some males but then with only 2 clavomeres. Pronotum not medially divided (Fig. 89). Ovipositor sheaths not expanded.

Discussion. Next generation molecular data (Cruaud et al., submitted) place *Trigonoderopsis* Girault and *Bugacia* Erdős new placement in Colotrechninae, as the sister group of Colotrechnini, instead of their previous placements in Pireninae or (in the case of *Bugacia*) dubiously in Ormocerinae. The reduced antennal flagellum helps diagnose this emergent group, and the relatively large mandible with 4 mandibular teeth may also help diagnose the tribe, although this feature is variable in Pteromalidae.

Erixestinae Burks & Rasplus, new subfamily

https://zoobank.org/49F28424-4F14-4E6E-8FDF-4ED6C5171747

Type genus. *Erixestus* Crawford, 1910.

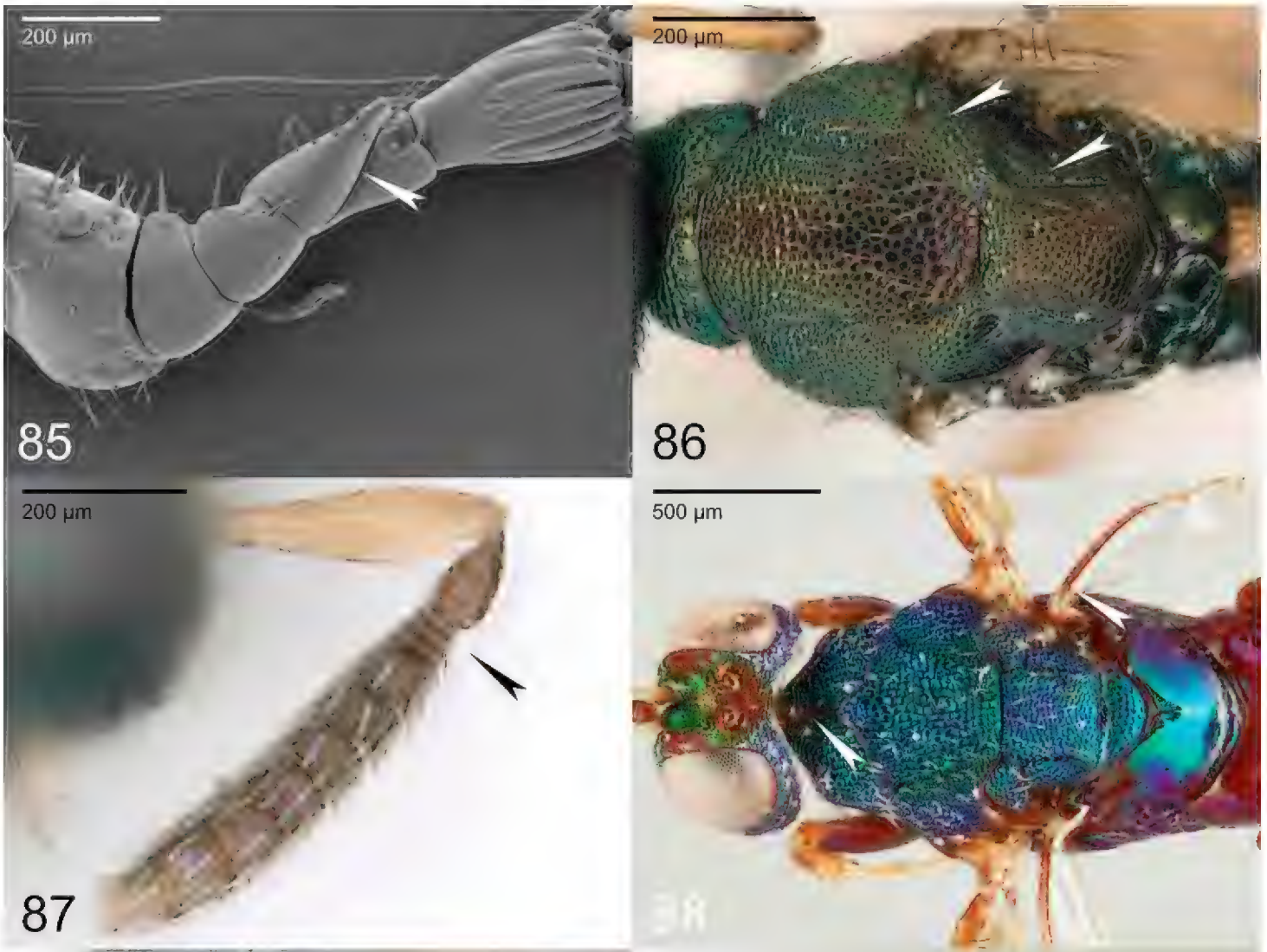
Diagnosis. Antenna with 11 flagellomeres, with 2 anelli and 5 funiculars (Fig. 90). Mandibles falcate. Scapula not anteriorly exposed by pronotum. Axilla not strongly advanced. Axillula not enlarged (Fig. 91). Propodeum with plicae. Petiole transverse.

Discussion. *Erixestus*, containing egg parasitoids of Chrysomelidae, had persisted in uncertain placement since its description, but had apparent affinities with Ormocerini due to the high dorsal placement of the toruli. Next-generation molecular data (Cruaud et al., submitted) suggest that it is the sister group of Pteromalinae plus Pachyneurinae. The falcate mandibles of Erixestinae and Pachyneurinae indicate that this may be a synapomorphy of this entire clade, rather than a synapomorphy of Pachyneurinae alone. Otherwise, features such as the subforaminal bridge do not reject the placement of Erixestinae, but the reduced flagellomere count would be very unusual, though not unknown in the clade. It is likely that divergent features of Erixestinae are due to a life history as egg parasitoids of Chrysomelidae.

Miscogastrinae

Miscogasteridae Walker, 1833. Type genus: *Miscogaster* Walker, 1833. Treated as Miscogasterinae by Ashmead (1904). Spelling corrected to Miscogastrinae by Burks (2012).

Diagnosis. Antenna nearly always with 12 flagellomeres (exception: *Andersena* Bouček). Mandibles usually not falcate, but sometimes enlarged (*Diconocara* Dzhanokmen). Scapula not anteriorly exposed by pronotum. Axilla not strongly advanced. Axillula rarely enlarged, but if so then they are not convex. Propodeum with or without plicae. Petiole variable, either with anterolateral flange extending from ventral surface to form lateral tooth-like protrusions (Fig. 97), or simple. If petiole simple, then clypeal margin asymmetrical (Fig. 94), or concave ventrally and then clypeus enlarged and nearly adjacent to toruli dorsally (Fig. 92).



Figures 85–90. 85 *Blastophaga psenes* (L.) (Agaonidae): antenna part **86** *Bofuria* sp. (Pteromalidae, Colotrechninae): mesosoma dorsal view **87** *Yrka* sp. (Pteromalidae, Colotrechninae, Amerostenini): antenna **88** *Divna hirsuta* Bouček (Pteromalidae, Colotrechninae, Divnini): mesosoma dorsal view **89** *Bugacia* sp. (Pteromalidae, Colotrechninae, Trigonoderopsini) **89** mesosoma dorsal view **90** *Erixestus* sp. (Pteromalidae: Erixestinae): antenna.

Discussion. Distinction of Miscogastrinae from Pteromalinae is best done by tribe, using either the distinctive petiole of Sphegigastrini or the distinctive clypeus of Diconocarini or Miscogastrini. We propose keeping these tribes together as Miscogastrinae, because they form a stable clade in molecular analyses (Cruaud et al., submitted), and because Sphegigastrini also can have an asymmetrical clypeus as in Miscogastrini.

Diconocarini Rasplus, Tselikh & Burks, new tribe

https://zoobank.org/FFB225F9-1C7F-4735-8B26-CE95F81316DC

Type genus. *Diconocara* Dzhanokmen, 1986.

Diagnosis. Clypeal margin concave, symmetrical (Fig. 92). Mandibles enlarged. Petiole small but subquadrate, without anterolateral carina (Fig. 93), ventrally narrowly connected and without a flange.

Discussion. *Diconocara* was described as an enigmatic member of Pteromalinae from the Russian Far East (Dzhanokmen 1986). Its position was unclear based on morphology (Heraty et al., 2013), although next-generation molecular data indicate that it is the sister group of all other Miscogastrinae (Cruaud et al., submitted). It does not have any obvious near relatives within Pteromalidae but also bears no resemblance to any other taxa outside Pteromalidae.

Miscogastrini

Diagnosis. Clypeal margin asymmetrical, with 2 or 3 teeth (Fig. 94). Mandibles not enlarged. Petiole variable in length but usually elongate, without the anterolateral carina of Sphegigastrini but often with a small lateral process that does not extend anteriorly (Fig. 95), ventrally either with a membranous gap medially or fused but without a flange.

Discussion. Miscogastrini comprise some of the most easily recognizable miscogastrines, large-bodied and usually with an expanded fore wing stigma.

Sphegigastrini

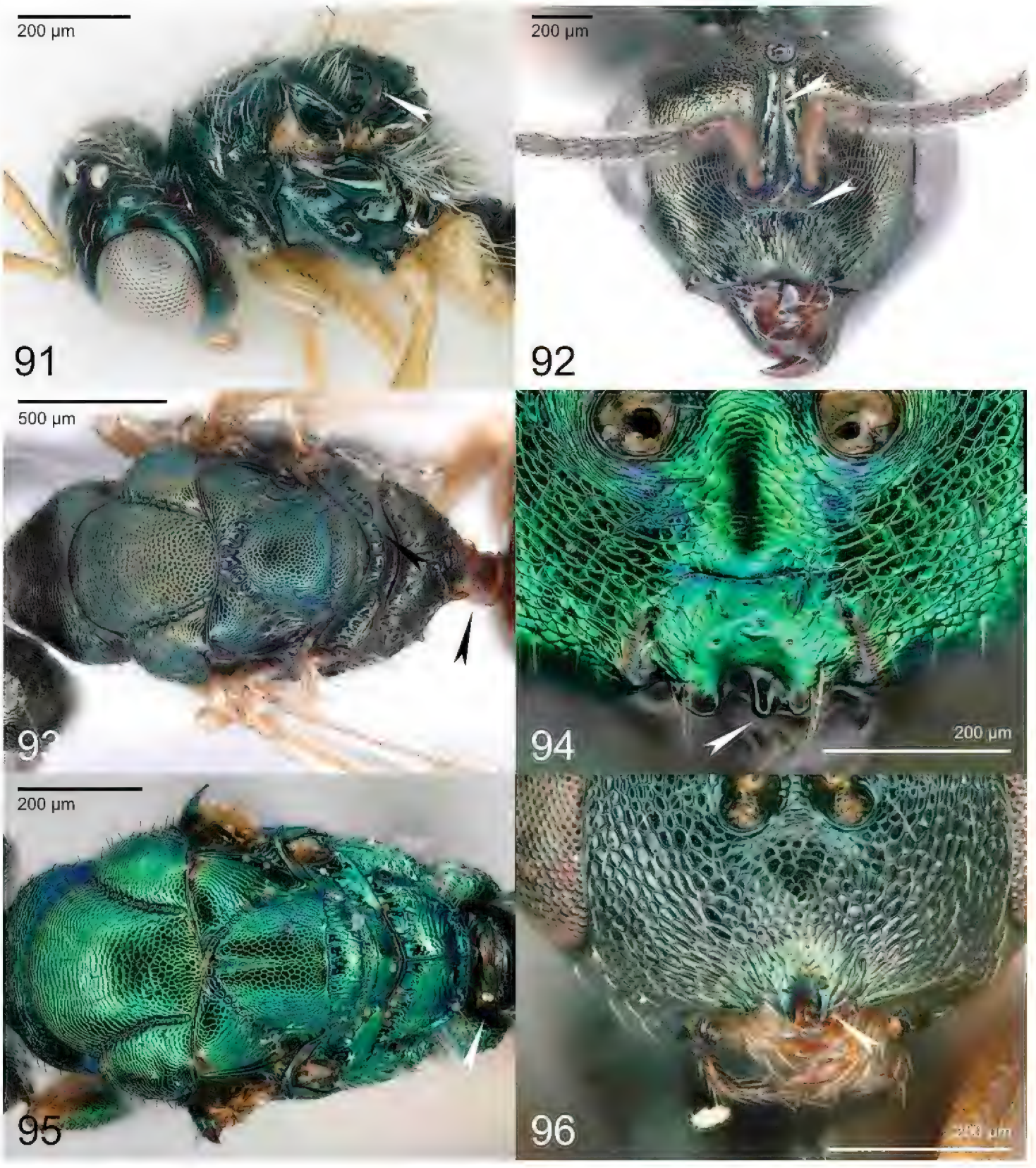
Sphegigastrides Thomson, 1876. Type genus: *Sphegigaster* Spinola, 1811.

Diagnosis. Clypeal margin symmetrical or asymmetrical, with 2 or 3 denticles or uniformly convex (Fig. 96). Mandibles not enlarged. Petiole usually elongate (exception: *Tricyclomischus* Graham), with anterolateral flange that extends anteriorly to flank petiolar insertion (Fig. 97), ventrally closed by the continuation of this flange.

Discussion. The current concept of Sphegigastrini agrees with that presented by Heydon (1988). Specimens of *Bairamlia fuscipes* Waterston new placement were examined morphologically in the course of this study, and were found to belong unambiguously to Sphegigastrini based on the anterolateral petiolar carina. Other genera that we place in Sphegigastrini, based on molecules and/or morphology, are listed in Appendix I.

Ormocerinae

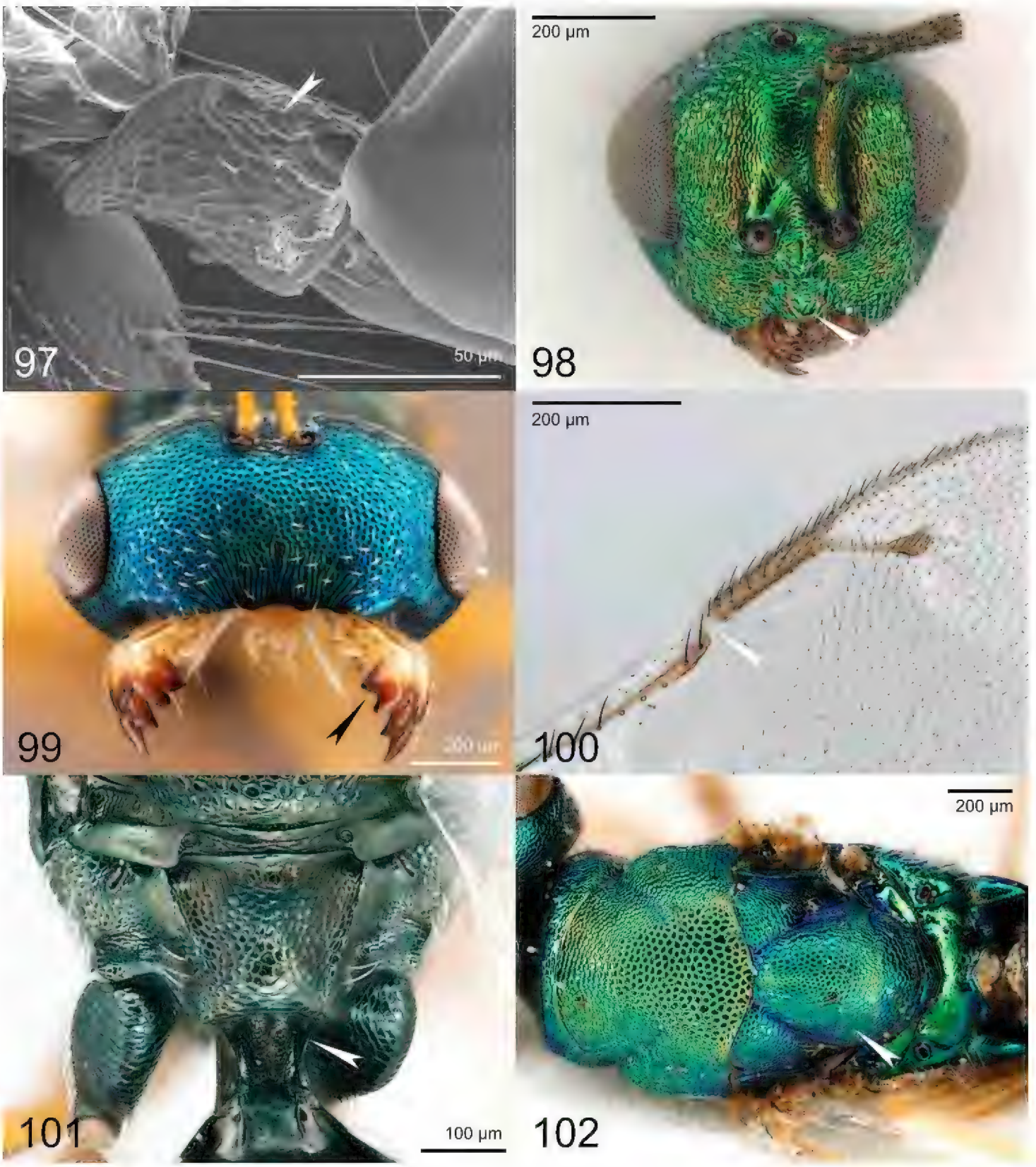
Ormoceridae Walker, 1833. Type genus: *Ormocerus* Walker, 1834. Treated as Ormocerinae by Bouček (1988).



Figures 91–96. 91 *Erixestus winnemana* Crawford (Pteromalidae, Erixestinae): mesosoma lateral view **92, 93** *Diconocara petiolata* Dzhanokmen (Pteromalidae, Miscogastrinae, Diconocarini) **92** head frontal view **93** mesosoma dorsal view **94, 95** *Thektogaster aberlenci* Delvare (Pteromalidae, Miscogastrinae, Miscogastrini) **94** clypeus **95** mesosoma dorsal view **96** *Sphegigaster obliqua* Graham (Pteromalidae, Miscogastrinae, Sphegigastrini): lower face frontal view.

Diagnosis. Antenna with 12 flagellomeres. Clypeal margin symmetrical, truncate or uniformly slightly convex (Fig. 98). Mandibles not enlarged. Scapula not anteriorly exposed by pronotum. Notauli complete. Axilla not strongly advanced. Axillula not enlarged. Propodeum without plicae. Petiole transverse, without anterolateral carina.

Discussion. The previous concept of Ormocerinae contained three additional tribes that are now recognized as separate groups in diverse lineages: Melanosomellidae,



Figures 97–102. 97 *Halticoptera* sp. (Sphegigastrini): petiole **98** *Ormocerus latus* Walker (Pteromalidae, Ormocerinae): head frontal view **99** *Acroclisoides sinicus* (Huang & Liao) (Pteromalidae, Pachyneurinae): head frontal and mandibles **100, 101** *Pachycrepoideus* sp. (Pachyneurinae) **100** venation **101** propodeum and petiole dorsal view **102** *Chlorocytus scandolensis* Rasplus (Pteromalidae, Pteromalinae): mesosoma dorsal view.

Systasidae, and the *incertae sedis* tribe Keryini (Bouček 1988; Gauthier et al. 2000). While there was some morphological resemblance between these groups, especially in the position of the toruli and in general gestalt, it became clear that they differed in many ways morphologically, as described in their given sections. Molecular data have suggested that the differences between these groups outweigh their similarities, and indeed Melanosomellidae is morphologically (see discussion of Melanosomellidae in its section above) and molecularly more similar to other members of the Gall Clade

(including Cynipencyrtidae, Epichrysomallidae, Ormyridae, and Tanaostigmatidae) than to other former Ormocerinae. Additionally, *Ormocerus* Walker is much more similar to Pteromalinae than to the aforementioned tribes. This resemblance is strongest with relatively generalized taxa such as *Nodisoplata* Graham new placement that is transferred here from Miscogastrini. The features comprising this resemblance are largely those of gestalt, including enlarged but flat axillula and the nearly equal lengths of fore wing marginal and stigmal veins. The other former members of Ormocerinae, Systasidae and Keryini, are more enigmatic in placement, but differ from the new concept of Ormocerini in features covered in their sections.

Cecidoxenus Ashmead new placement is transferred here from its former position in what is now Melanosomellidae, because of its strong morphological resemblance to *Ormocerus* although with a slightly longer marginal vein. Additionally, *Blascoa* Askew new placement and *Monazosa* Dzhanokmen new placement are transferred here based on morphology.

Ormocerinae strongly resemble some genera of Pteromalini (Pteromalinae) that are retained with some doubt in their current classification because they have not been analyzed molecularly, such as *Fijita* Bouček and *Huberina* Bouček. They differ from Ormocerinae as characterized here by either having features that are conspicuously different from those of ormocerines, such as a median clypeal tooth or pair of teeth, a propodeum with plicae, or an elongate petiole. Other Pteromalinae with complete notauli are fig associates (Otitesellini) that have very different fore wing venation from Ormocerinae.

Pachyneurinae new status

Pachyneurini Ashmead, 1904. Type genus: *Pachyneuron* Walker, 1833.
Austroterobiinae Bouček, 1988 new synonymy. Type genus: *Austroterobia* Girault, 1938.

Diagnosis. Antenna with 12 flagellomeres. Mandibles falcate (Fig. 99). Scapula not anteriorly exposed by pronotum. Axilla not strongly advanced. Axillula not enlarged. Fore wing marginal vein abruptly thickened at parastigmal break relative to submarginal vein thickness (Fig. 100). Propodeum with or without plicae. Petiole (when distinct) anteroventrally either braced by a flange extending from the 1st gastral sternum that reaches anteriorly under the petiolar attachment, e.g. *Pachycrepoideus* Ashmead (Fig. 101), or with a more or less developed lateral tooth-like process that extends perpendicular with the longitudinal axis of the petiole, e.g. *Pachyneuron* Walker.

Discussion. Austroterobiinae new syn. was described to contain morphologically divergent parasitoids of margarodid scales (Hemiptera). However, during this study it was observed that they have a recessed subforaminal bridge as in Pteromalinae and Pachyneurinae. Next generation molecular data (Cruaud et al., submitted) place austroterobiines as a derived group inside Pachyneurinae. Although *Austroterobia* Bouček and *Teasienna* Heydon are morphologically divergent from other Pachyneurinae in having complete notauli, this can be attributed to the switch to Margarodidae as hosts. *Austroterobia* and *Teasienna* agree with other Pachyneurinae in having falcate mandi-

bles. Given the derived position of these genera within Pachyneurinae, we see no value in preserving the group as a tribe. Other genera transferred to Pachyneurinae, based on molecules and/or morphology, are listed in Appendix 1.

Pteromalinae

Diagnosis. Antennal nearly always with 12 flagellomeres (exceptions: some Otitesellini, *Amphidocius* Dzhanokmen, possibly *Termolampa*). Mandibles usually not falcate (exceptions include some *Apsilocera* Bouček and *Kaleva* Graham). Scapula not anteriorly exposed by pronotum. Notauli usually incomplete, but if complete then clypeus with median tooth or teeth, propodeum with plicae, or petiole distinct and not strongly transverse, e.g., *Fijita*. Axilla variable but usually not strongly advanced (exceptions: *Manineura* Bouček). Axillula usually not enlarged (Fig. 102), but if enlarged then not convex. Fore wing with marginal vein usually slender, if distinctly thickened, e.g. *Rhaphitelus* Walker, then mandibles not falcate. Petiole simple or with small anterolateral processes.

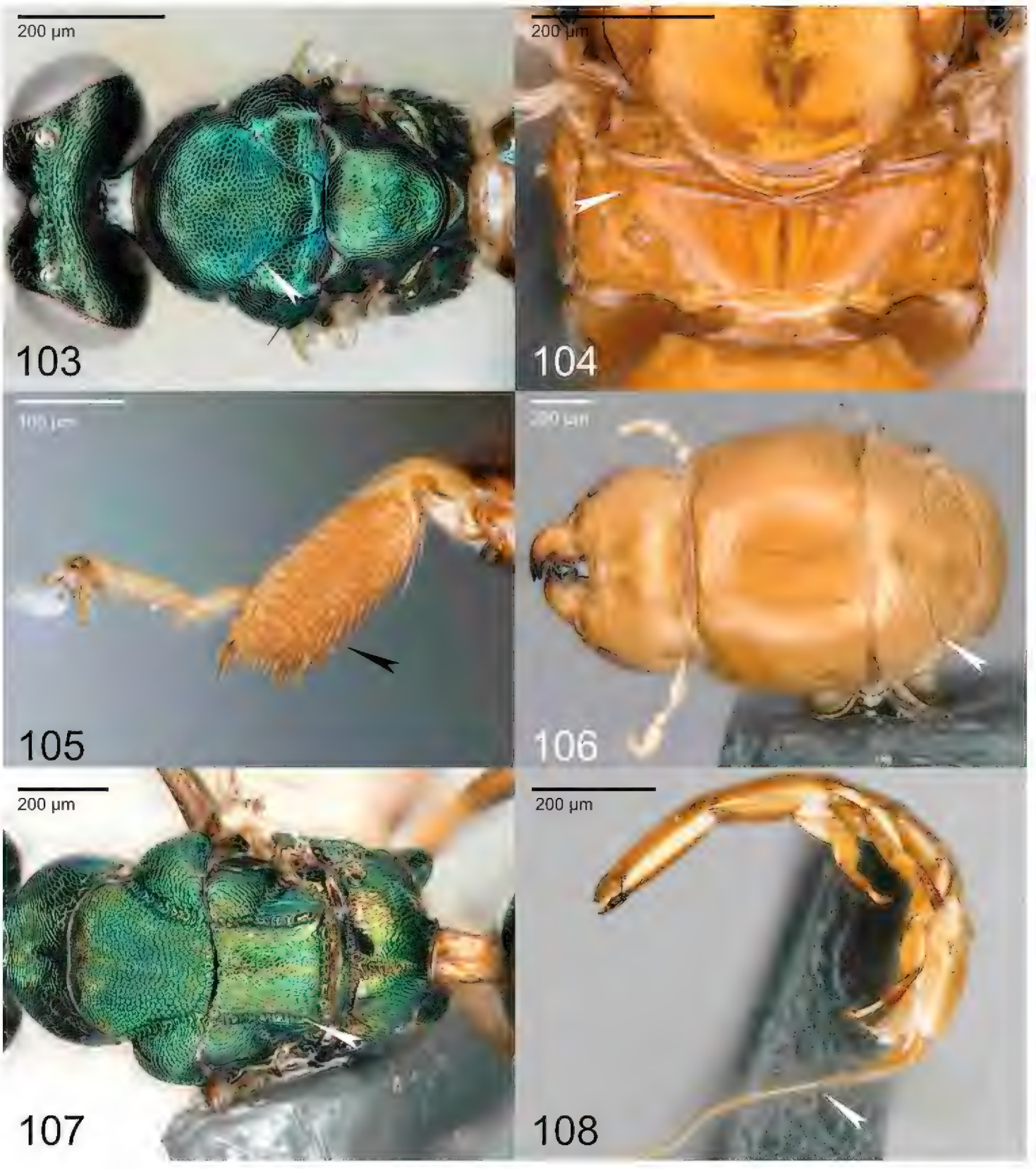
Discussion. Pachyneurinae differ from Pteromalinae in having a combination of falcate mandibles and an abruptly thickened marginal vein base immediately apical to the parastigmal break. Ormocerinae resemble some genera of Pteromalini that are retained with some doubt, but which differ from ormocerines in a number of respects discussed above. The few petiolate Pteromalinae differ from Miscogastrinae as follows: from Diconocarini in having small mandibles; from Miscogastrini in the symmetric clypeus; and from Sphegigastrini in the petiole structure, such as the lack of the characteristic anterolateral petiolar carina.

Otitesellini new status

Otitesellini Joseph, 1964. Type genus: *Otitesella* Westwood, 1883.
Sycoryctini Wiebes, 1966 new synonymy. Type genus: *Sycoryctes* Mayr, 1885.
Sycoecini Hill, 1967 new synonymy. Type genus: *Sycoecus* Waterston, 1914.

Diagnosis. Antenna with 10 flagellomeres (*Diaziella* Grandi, *Marginalia* Priyadarsanan, *Robertsia* Bouček, *Seres* in part, *Sycoecus*), 11 flagellomeres (*Apocrypta* Coquerel, *Arachonia* Joseph, *Seres* in part, *Otitesella*, *Walkerella* Dalla Torre) or 12 flagellomeres (other genera). Notauli mostly complete (Fig. 103) (absent in *Seres*). Propodeal spiracle usually separated from the anterior propodeal margin by about their own length, or more (except *Marginalia*, some *Walkerella* and *Robertsia*) (Fig. 104). Males usually apterous (except in most members of previous Sycoecinae, some *Watshamiella* Wiebes, and *Sycoryctes* Mayr).

Discussion. This tribe of Pteromalinae contains the previously recognized subfamilies Otitesellinae, Sycoecinae new syn. and Sycoryctinae new syn., all fig associates occurringin the Old World (about 30 genera). It does not contain all the fig associates in Pteromalidae, since Sycophaginae is a separate subfamily of fig associates,



Figures 103–108. 103 *Apocrypta caudata* (Girault) (Pteromalidae, Otitesellini): mesosoma dorsal view **104** *Philotrypesis caricae* L. (Otitesellini): propodeum **105** *Seres wardi* van Noort (Otitesellini): fore tibia **106** *Grandiana* sp. (Otitesellini): male dorsal view **107** *Pseudidarnes minerva* Girault (Pteromalidae, Sycophaginae): metasoma dorsal view **108** *Sycophaga* sp. (Pteromalidae, Sycophaginae): male lateral view.

Podivna Bouček is classified in Colotrechninae, and some New World genera (*Critogaster* Mayr, *Aepocerus* Mayr, *Heterandrium* Mayr, and similar genera) belong to another group of Pteromalinae. Otitesellini possess an amazing morphological disparity. Some genera that enter the fig through the ostiole have a flattened head and smooth cuticle, as well as adaptations to crawl through the bracts filling the fig aperture (mandible lengthened and covered with multiple small teeth, spurs on fore- and hind

legs, enlarged protibial spur etc.) (Fig. 105). Some others oviposit within flowers from the outside once the fig is enlarged and therefore have elongated valves, or with last two tergites lengthened. Most males are greatly transformed, often apterous and sometimes with enlarged mandibles and scapes that are used for fighting for females (Fig. 106). Other genera that we place in Otitesellini based on molecules and/or morphology are listed in Appendix 1.

Pteromalini

Termolampini Bouček, 1961 new synonymy. Type genus: *Termolampa* Bouček, 1961.

Discussion. The previously recognized tribe Termolampini new syn. is abolished here, because it can only be distinguished from other Pteromalini using features that define the genus, and because it seems to be a derived genus within Pteromalini, instead of the sister group of another tribe or set of tribes in Pteromalinae. To resolve previous confusion, *Boucekina* Szelényi new placement and *Morodora* Gahan new placement belong here according to their morphological resemblance to other Pteromalini, respectively *Neanica* Erdős and *Perniphora* Ruschka. The complete list of genera of Pteromalini are listed in Appendix I, based on molecules and/or morphology. At present the tribe is not diagnosed, because it is the remainder of Pteromalinae excluding Otitesellini. The vast remaining number of genera in Pteromalini makes it unwieldy, and future analysis will be needed to break it up into useful natural tribes that can be more easily diagnosed.

Sycophaginae new placement

Sycophagoidae Walker, 1875. Type genus: *Sycophaga* Westwood, 1840. Treated as Sycophaginae by Ashmead (1904).

Diagnosis. Antennal variable in flagellomere count. Mandibles not falcate. Scapula anteriorly exposed by narrow pronotum. Axilla not strongly advanced. Axillula enlarged and convex (Fig. 107). Petiole simple, transverse. Males usually apterous (except in a few genera), residing inside figs (Fig. 108).

Discussion. The taxonomic placement of the subfamily Sycophaginae has long been controversial. Sycophaginae were previously classified in Torymidae (Wiebes, 1967) and Agaonidae (Bouček 1988; Heraty et al. 2013) as the family shares at least few features with these families. Different strategies to reduce biases in our phylogenetic inference (Cruaud et al., submitted) stabilized the position of Sycophaginae as sister to all other Pteromalidae. This position is corroborated by several features shared with other members of the family and a few others shared with Colotrechninae (large and convex axillula), the next lineage in the Pteromalidae topology. Sycophaginae and Colotrechninae also share a gall-associated biology, indeed most Sycophaginae are ei-

ther gall-makers or parasitoids of gall-makers within figs. We therefore propose to include Sycophaginae in Pteromalidae new placement.

Trigonoderinae new status

Trigonoderini Bouček, 1964. Type genus: *Trigonoderus* Westwood, 1832.

Diagnosis. Antenna with 12 flagellomeres. Mandibles often large but not falcate (Fig. 109). Scapula anteriorly exposed by narrow pronotum. Axilla hardly advanced. Axillula usually not enlarged, but if so (*Plutothrix* Förster), then it is not convex (Fig. 110). Petiole simple, usually transverse and hardly visible.

Discussion. Trigonoderinae are relatively distinctive pteromalids that differ from most others in the family in their long, large bodies in combination with complete notauli and a well-indicated frenal groove (displaced posteriorly in *Platygerrhus* Thomson). Many Pteromalinae are also large-bodied and can be confused superficially with Trigonoderinae, although they have incomplete notauli.

Nomenclatural changes in other chalcidoid families

Baeomorphidae new status

Baeomorphinae Yoshimoto, 1975. Type genus: *Baeomorpha* Brues, 1937. Synonymized with Rotoitidae Bouček & Noyes, 1987 (and inferred synonymy with Rotoitinae) by Gumovsky et al. (2018).

Discussion. The family group name Baeomorphinae was established by Yoshimoto (1975). Rotoitidae was established by Bouček and Noyes (1987). When the two groups were synonymized by Gumovsky et al. (2018), they invoked article 35.5 of the ICZN to conserve the family name Rotoitidae. However, as Baeomorphinae cannot be recognized as a subfamily independent of a Rotoitinae, the family name must be treated with priority and Baeomorphidae recognized over Rotoitidae.

Calesidae new status

Calesinae Mercet, 1929. Type genus: *Cales* Howard, 1907.

Diagnosis. Antenna with radicle 2–4 times as long as broad; 3 or 4 flagellomeres, clava fused and longer than preceding flagellomeres; most species with multiporous plate sensilla raised and not attached along length to flagellomeres. Protibial spur short and straight. All legs with 4 tarsomeres. Axilla extending forward as distinct narrow

scapula (Fig. 111). Mesosoma broadly joined to metasoma, with second phragma extending into metasoma. Hind wing with strongly curved marginal vein. Body pale yellowish or yellowish brown in color.

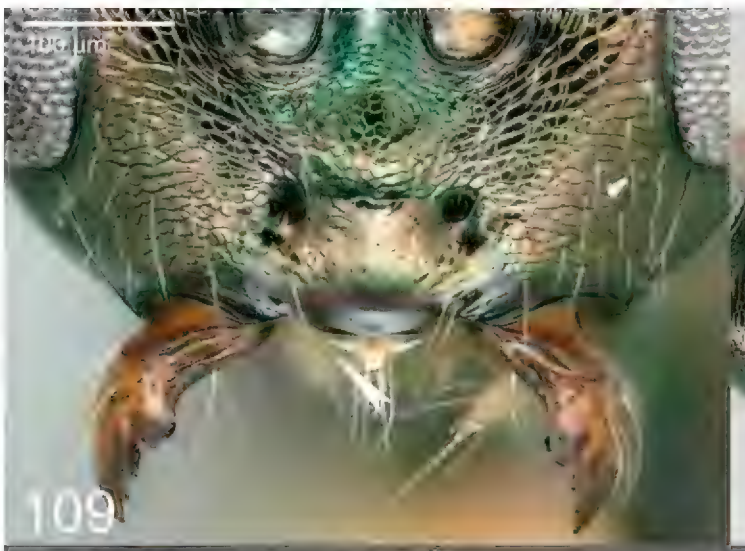
Discussion. Calesinae has been treated as an unusual component of Aphelinidae with no direct affinities to other Aphelinidae (Mottern et al. 2011; Heraty et al. 2013). Next generation molecular data conclusively place the only genus *Cales* Howard as part of a sister group to most other lineages of Chalcidoidea (Cruaud et al., submitted) and not as a member of Aphelinidae. Given that Calesidae is divergent from Aphelinidae both morphologically (Fig. 111) and molecularly, we raise it to family status. Calesidae resemble many Trichogrammatidae in features of the fore wing venation and antennae, but differ from this family by having 4-segmented tarsi. Euderomphalini (Eulophidae) are similar whitefly parasitoids, but these can be distinguished by their narrow petiole with the second phragma restricted to the mesosoma.

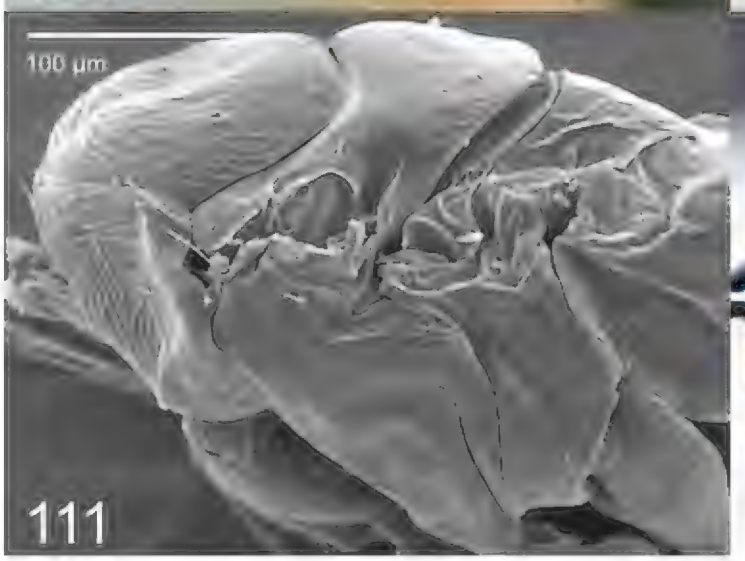
Eulophidae

Discussion. The family Eulophidae is not diagnosed here since its limits are not being adjusted, but some taxonomic changes have been carried out as a result of our studies. The Australasian tribe Platytetracampini was described in Entedoninae by Bouček (1988), placed there because of general resemblance to some Euderomphalini. Its placement has been treated as debatable in part because of the relatively large flagellomere count (Bouček 1988; Gauthier, et al. 2000), and it was found to be the sister group of Anselmellini, in what is now Opheliminae, a phylogenetic analysis of 28S D2 ribosomal DNA by Gauthier et al. (2000) and Gumovsky (2002). We suggest that Platytetracampini should be treated as a tribe in Opheliminae new placement, because *Platytetracampe* Girault shares with other ophelimines the placement of fore wing admarginal setae on the ventral side of the marginal vein, and because this transfer renders Entedoninae more definable morphologically, agreeing better with Opheliminae. Although this placement of the admarginal setae is not unique in Eulophidae, we suggest that it may be locally informative for Opheliminae. More definitive placement awaits analysis of next-generation molecular data for *Platytetracampe*, which so far has not been available.

Boucekelimini is a morphologically distinctive group that was treated as an unplaced tribe in Eulophidae by Kim & La Salle (2005). Molecular data for this tribe have not been available, but based again on the placement of the admarginal setae on the ventral side of the marginal vein, and upon the similarity of the antenna of *Boucekelimus* Kim & La Salle (cf. fig. 2) and fore wing stigma shape (Kim and La Salle 2005: figs 11, 12, 19, 20) with that of *Ophelimus* Haliday, we treat Boucekelimini as a tribe within Opheliminae new placement, again awaiting next-generation molecular data for further evaluation of the phylogenetic value of morphological features mentioned here.

Elasmus Westwood was treated in a separate family until molecular data (Gauthier et al. 2000) suggested that it is part of Eulophinae. Elasmini was therefore reduced to tribe rank within Eulophinae. Rasplus et al. (2020) later found using next-generation





Figures 109–114. 109, 110 *Gastracanthus acutus* (Kamijo) (Pteromalidae, Trigonoderinae) **109** lower face frontal view **110** mesosoma dorsal view **111** *Cales noacki* Howard (Calesidae): mesosoma lateral view **112** *Eusandalum flavipenne* Ruschka: mesosoma dorsal view **113** *Pentacladia elegans* Westwood: Mt8 and Mt9 fused, but delimited by an oblique suture below cercus **114** *Chromeurytoma* sp. (Megastigmidae, Chromeurytominae): head and mesosoma dorsal view.

UCE molecular data that *Sympiesis* Foerster is the sister group of *Elasmus*, rendering recognition of Elasmini problematic versus the now paraphyletic Eulophini, especially since *Sympiesis* is very similar to many other genera of Eulophini morphologically. Given that males of *Elasmus* have branched flagellomeres very much like those of Eulophini, we find the recognition of a separate Elasmini to be an unjustifiable misrepresentation

of the evolutionary timing of the distinctive traits of *Elasmus* relative to the traits that are representative of Eulophini, and therefore Elasmini new syn. is a synonym of Eulophini.

Gyrolasomyiini was described as a separate tribe of Tetrastichinae by Bouček (1988). Molecular data have so far placed *Gyrolasomyia* Girault within Tetrastichini, with instead a *Tetrastichus*-group (Rasplus et al. 2020) being the sister group of remaining Tetrastichinae: the *Aprostocetus*-group including *Gyrolasomyia*. Therefore, recognition of Gyrolasomyiini would necessitate recognition of a separate tribe for the *Aprostocetus*-group or synonymy of Gyrolasomyiini with the oldest available tribe name of the *Aprostocetus*-group. However, this is untenable due to the highly problematic morphological diagnosability of tetrastichine genera and potential tribes. We suggest that both uncertain phylogenetic relationships and the practical difficulties of diagnosing subordinate taxa make recognition of tribes in Tetrastichinae currently inadvisable, and therefore Gyrolasomyiini new syn. is a junior synonym of Tetrastichini.

Eupelmidae

Eusandalinae Fusu, new subfamily

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Type genus. *Eusandalum* Ratzeburg, 1852.

Diagnosis. Antennal flagellum with 9 flagellomeres, clava undivided. Eyes ventrally divergent. Clypeus with truncate apical margin. Labrum subquadrate, exposed. Subforaminal bridge with median area flanked by elongate posterior tentorial attachments; postgenal bridge externally separates the lower tentorial bridge from the hypostomal carina; postgenal groove and postgenal lamina absent. Anterolateral mesoscutal corners projecting shoulder-like on either side of the pronotum (a feature shared with Calosotinae *sensu stricto*). Notauli superficial and convergent, and except for *Archaeopelma*, ending about halfway across mesoscutum (Fig. 112). Axilla approximated (*Archaeopelma* Gibson and *Paraeusandalum* Gibson) or widely separated (*Eusandalum* Ratzeburg, *Licrooides* Gibson and *Pentacladia* Westwood) medially. Axillular groove or carina absent. Frenum absent. Acropleuron expanded and forming the largest surface of the mesopleuron, either comparatively small and not reaching metapleuron and metacoxa (*Archaeopelma*, *Licrooides*) or occupying most of the visible part of the mesopleuron and extending to the metapleuron (the other three genera). All legs with 5 tarsomeres; protibial spur stout and curved; basitarsal comb longitudinal; ventral membranous area anterior to mesocoxal attachment present; mesotibial spur stout except only slightly thickened in *Archaeopelma*. Fore leg with protibial dorsal spicules (except in *Licrooides*). Mesotarsus almost never with row of pegs along both sides, the exception being *Licrooides*: with spine-like setae on both antero- and posteroventral margins (*Archaeopelma*) or a row of pegs on posteroventral margin and a row of spine-like setae along anteroventral margin (remaining three genera). In *Licrooides* there are robust spines on both margins that almost appear as pegs. Metasoma in females with separate Mt8 and Mt9, hence without syntergum (*Eusandalum*) or with Mt8 and Mt9

fused but delimited by a transverse suture between cerci (*Archaeopelma*) or below each cercus (remaining genera; Fig. 113). Sexual dimorphism reduced, limited mainly to primary sexual features and antennal structure.

Discussion. Eusandalinae new subfamily were treated until now as part of Calosotinae, however in next-generation molecular analyses (Cruaud et al., submitted) they were never recovered as monophyletic with the other Calosotinae. Instead, a reduced group of Calosotinae that includes *Balcha* Walker, *Calosota* Curtis and *Tanythorax* Gibson (Calosotinae *sensu stricto*) are sister to *Heydenia* (Heydeniidae) in all final analyses and closer to Eupelminae than to Eusandalinae. Eusandalinae are part of the same large clade containing also the Eupelminae and Calosotinae, but the three Eupelmidae subfamilies never form a monophyletic group since the clade also includes Ditropinotellinae, Heydeniidae and Solenurinae; Eusandalinae are the basal group. Beside the three genera included in these molecular analyses (Cruaud et al., submitted) we also include in Eusandalinae *Archaeopelma* and *Licrooides* based on a UCE analysis with a larger sampling (unpublished data). A possibly biphyletic Calosotinae *sensu lato* was also recognised by Gibson (1989), however with *Licrooides* hypothesized as closer to *Calosota* and allied genera and not to *Eusandalum*, and *Archaeopelma* as the most basal lineage of all Calosotinae. From the morphologically close Calosotinae *sensu stricto*, the Eusandalinae differ mainly in having an undivided clava, convergent notauli, scutellum without axillular groove or carina, mesotarsus almost never with two fully developed rows of pegs and a metasoma with incompletely fused or independent Mt8 and Mt9. In Calosotinae: clava with three clavomeres, notauli present as paramedially parallel lines, axillular groove present and continuing seamlessly with the scuto-scutellar suture and as a result scutellum with a carinated groove extending from base to apex, mesotarsus with a row of pegs on either side, and Mt8 and Mt9 completely fused to form the syntergum. However, all the characteristic features of Eusandalinae are either plesiomorphic or homoplastic. A thorough comparative analysis of all these characters can be found in Gibson (1989).

Khutelchalcididae new placement

Khutelchalcididae Rasnitsyn, Basibuyuk & Quicke, 2004. Type genus: *Khutelchalcis* Rasnitsyn, Basibuyuk & Quicke, 2004.

Discussion. Khutelchalcididae was described as a new family of Chalcidoidea from a compression fossil at an estimated age of around the Jurassic/Cretaceous boundary (Rasnitsyn et al. 2004). Gibson et al. (2007) rejected the placement of Khutelchalcididae in Chalcidoidea on the grounds that the position of the mesothoracic spiracle is not in the location that is apomorphic for Chalcidoidea, but is instead in a position similar to that in Serphitidae. We follow the conclusion from Gibson et al. (2007) here, and officially exclude Khutelchalcididae new placement from Chalcidoidea, to be retained in Apocrita as an *incertae sedis* taxon that is not placed to superfamily.

Megastigmidae

Megastigmidae Thomson, 1876. Type genus: *Megastigmus* Dalman, 1820.
Chromeurytominae Bouček, 1988 new placement. Type genus: *Chromeurytoma* Cameron, 1912.
Keiraninae Bouček, 1988 new placement. Type genus: *Keirana* Bouček, 1988.

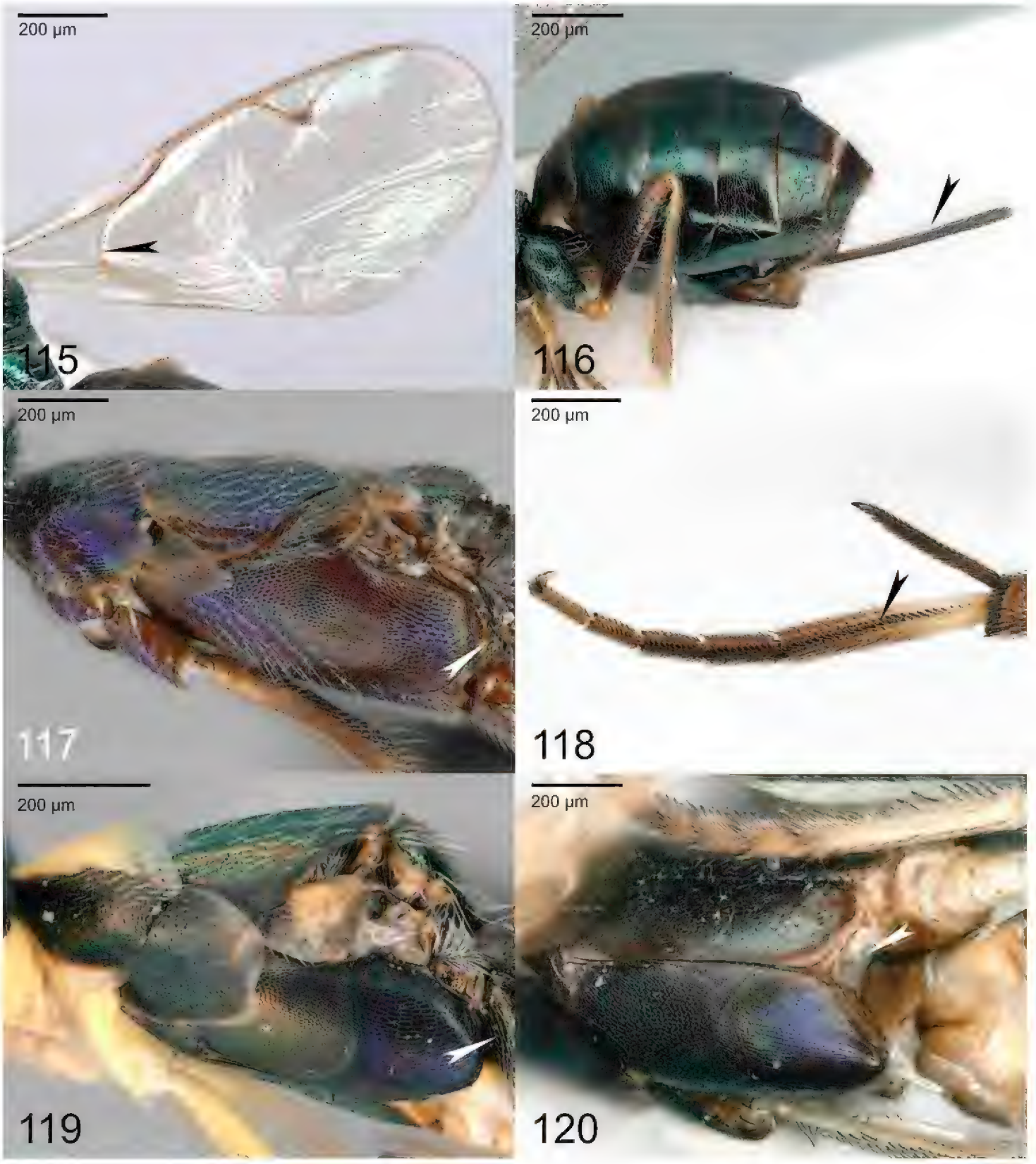
Diagnosis. Antenna with 10 (*Chromeurytoma*) or 12 (Megastigminae and Keiraninae) flagellomeres, including a 4th clavomere. Eyes not or only slightly divergent ventrally. Clypeus bilobed or medially produced, without transverse subapical groove. Labrum flexible and mostly or entirely hidden behind clypeus, divided into several small lobes or subtriangular. Mandibles with 3 teeth. Occipital carina present, at least dorsally in *Chromeurytoma* (Fig. 114), usually high on the head. Pronotum usually elongate, but about as long as mesoscutum or shorter in Chromeurytominae. Notauli complete. Mesoscutellum with frenum defined by a distinct frenal groove, with or without axillular sulcus (Fig. 114). Postmarginal vein longer than stigmal vein (excepted in *Patiyana* Bouček) and frequently longer than marginal vein. Basal fold usually pigmented, in a few genera developed into a basal vein curved outwards (Megastigminae and Keiraninae) (Fig. 115) or rarely basal fold hyaline (Chromeurytominae). All legs with 5 tarsomeres, protibial spur stout and curved; basitarsal comb longitudinal. Gaster, while sometimes rigidly convex, not strongly sclerotized; metasomal apex usually with a separate epipygium in females (in Chromeurytominae and Megastigminae) or with a syntergum that is crossed by a sulcus immediately anterior to the cerci (Keiraninae). Cerci elongate. Ovipositor sheaths long and upcurved in females (Fig. 116).

Discussion. Megastigminae had long been recognized as a monophyletic subfamily of Torymidae and has recently been upgraded to family rank (Janšta et al. 2018). Next-generation molecular analyses (Cruaud et al., submitted) have consistently suggested that two previous subfamilies of Pteromalidae (Chromeurytominae and Keiraninae) were closely related to Megastigmidae. Morphological examination of species of *Chromeurytoma* Cameron and *Keirana* Bouček has confirmed that these clades share several diagnostic features with Megastigmidae and belong to this family. Adding these two entities has increased the morphological disparity within Megastigmidae and has decreased the already low number of apomorphies that define the family. Consequently, Megastigmidae now comprises three subfamilies: Megastigminae including most megastigmid genera (Böhmová et al. 2022), Chromeurytominae new placement (including *Chromeurytoma*, *Asaphoideus* Girault and *Patiyana*) and Keiraninae new placement (with only *Keirana*).

Metapelmatidae revised status

Metapelma Bouček, 1988. Type genus: *Metapelma* Westwood, 1835.

Diagnosis. Antenna with 11 flagellomeres, including 3 clavomeres. Eyes ventrally divergent. Clypeus with truncate apical margin. Labrum subquadrate, exposed. Mandibles



Figures 115–120. 115, 116 *Keirana* sp. (Megastigmidae, Keiraninae) **115** wing **116** metasoma lateral view **117, 118** *Metapelma* sp. (Metapelmatidae) **117** mesosoma lateral view **118** apex of mesotibia and mesotarsus **119, 120** *Neanastatus* sp. (Neanastatidae) **119** mesosoma lateral view **120** mesosoma ventral view.

with a ventral tooth and a dorsal weakly emarginate truncation or with 3 teeth. Subforaminal bridge with postgenal bridge separating secondary posterior tentorial pits from hypostoma; hypostomal carina convergent. Axilla transverse, approximated medially. Mesoscutellum with apex rounded; axillular groove or carina present. Frenum absent. Acropleuron enlarged, convex and pad-like, covering most of mesopleural area but separated from metacoxa by mesepimeron and metapleuron (Fig. 117). All legs with 5 tarsomeres; protibial spur stout and curved; basitarsal comb longitudinal; ventral membranous area anterior to mesocoxal attachment absent; mesotibial spur stout;

mesotarsus with 1 row of pegs anteroventrally (Fig. 118). Metasoma with separate Mt8 and Mt9 in females, without syntergum.

Discussion. Next-generation molecular data (Cruaud et al., submitted) consistently place *Metapelma* Westwood far from its former position in what is now Neanastatidae, instead most frequently as the sister group of Macromesidae + Cleonymidae. There is only minor, and not consistently diagnostic, resemblance between these three groups, and therefore Metapelmatidae revised status is restored from synonymy as a separate family. The difference between Metapelmatidae and Neanastatidae is subtle but present, in that Neanastatidae do not have the mesopleural area separated from the metacoxa by the mesepimeron and metapleuron. *Eopelma* also differs in several respects, including having fewer flagellomeres with an undivided clava, and does not bear any resemblance to *Metapelma*. Eupelmidae differ in ways explained by Gibson (1989, 1995), but notably by having a membranous area anterior to the mesocoxal attachment ventrally. Male Eupelminae additionally do not have an expanded acropleuron and all the associated modifications of the mesosoma and mid legs.

Neanastatidae new status

Neanastatinae Kalina, 1984. Type genus: *Neanastatus* Girault, 1913.

Diagnosis. Antenna with 8, or sometimes apparently 7 flagellomeres in *Neanastatus*, or with 11 in *Lambdobregma* Gibson. Eyes ventrally divergent. Clypeus without transverse subapical groove. Labrum hidden behind clypeus, flexible. Mandibles with 3 teeth. Subforaminal bridge with postgenal bridge separating secondary posterior tentorial pits from hypostoma. Axilla transverse, approximated (*Lambdobregma*) or widely separated (*Neanastatus*) medially. Mesoscutellum with a downwards-projecting hook-like apex; axillular groove or carina present. Frenum apparently absent though the marginal rim of the mesoscutellum may be greatly expanded. Acropleuron enlarged, convex and pad-like; covering mesopleural area (Fig. 119). All legs with 5 tarsomeres; protibial spur stout and curved; basitarsal comb longitudinal; ventral membranous area anterior to mesocoxal attachment absent (Fig. 120); mesotibial spur stout; mesotarsus with 1 row of pegs anteroventrally. Metasoma with syntergum, therefore without epipygium.

Discussion. Neanastatidae, with only *Neanastatus* and *Lambdobregma* remaining, is not related to the formerly included genera *Metapelma* (Metapelmatidae) or *Eopelma* in next-generation molecular analysis (Cruaud et al., submitted). Even then, Neanastatidae is rendered paraphyletic by the *incertae sedis* taxon *Callimomoides* (Louriciinae). Metapelmatidae differ from Neanastatidae in a number of features, including the separate Mt9 in females and the separation of the acropleuron from the mesocoxa by the metapleuron and small mesepimeron in Metapelmatidae. The acropleuron is also separated from the mesocoxa in *Eopelma*, which nevertheless bears the greatest gestalt

resemblance to *Neanastatus* out of all these taxa due to size, coloration, and flagellomere count. Each of these genera differs from Eupelmidae in lacking a membranous area anterior to the mesocoxal attachment ventrally.

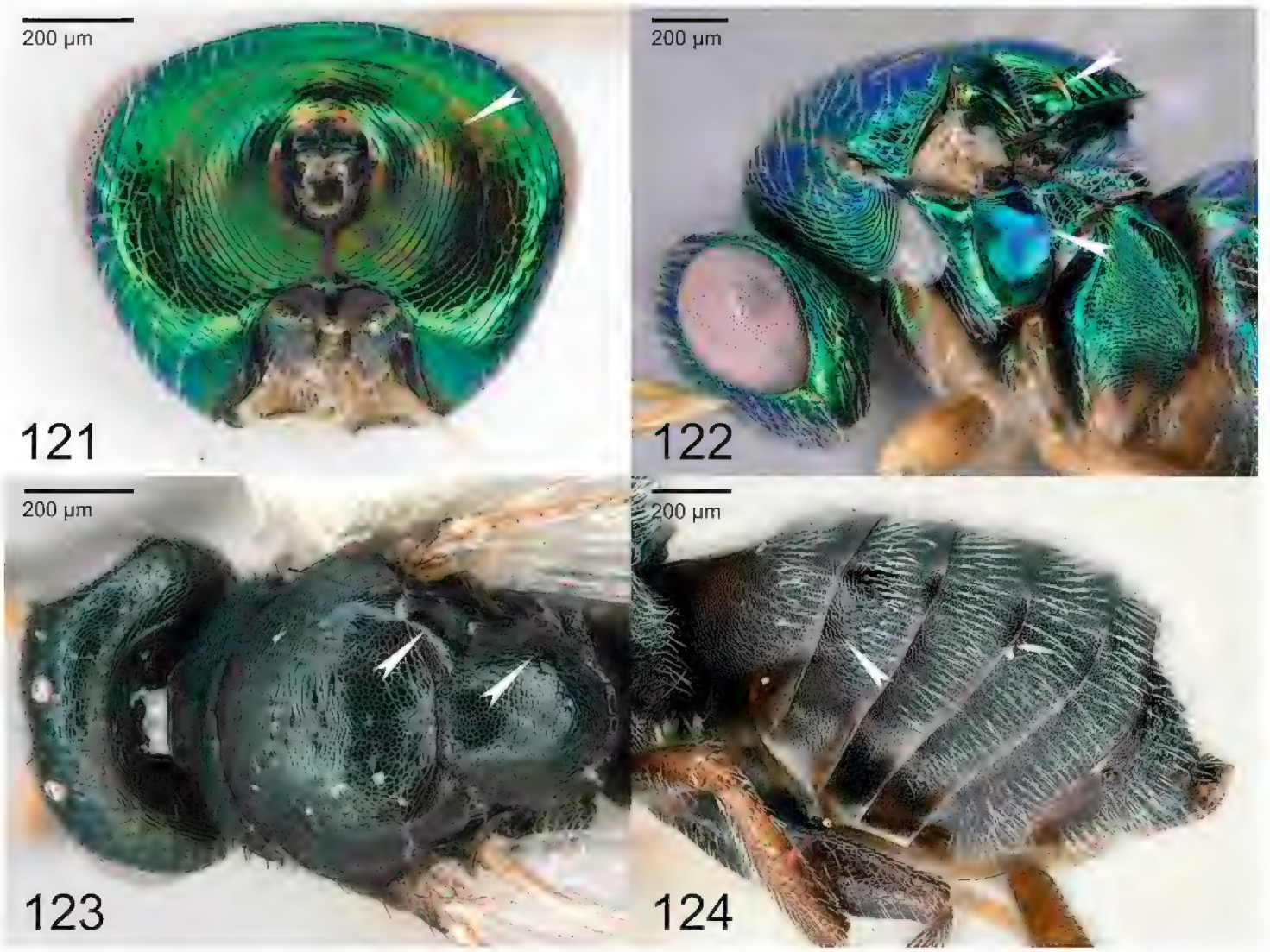
Ormyridae

Ormyridae Foerster, 1856. Type genus: *Ormyrus* Westwood, 1832.

Diagnosis. Antenna with 12 flagellomeres, including a small 4th clavomere. Eyes not ventrally divergent. Clypeus bilobed, without transverse subapical groove. Labrum hidden behind clypeus, flexible, subrectangular with marginal setae in a row. Mandibles with 2 or 3 teeth. Subforaminal bridge with postgenal lobe separating the secondary posterior tentorial pit from the hypostoma and restricting it to the vicinity of the occipital foramen; postgenal bridge present or separated (and therefore lower tentorial bridge reaching or not reaching hypostoma); postgenal lamina usually absent; hypostomal carina usually (but not always) convergent; occipital carina present (Fig. 121). Axilla advanced (Fig. 123). Mesoscutellum with frenum indicated at least laterally, without axillular sulcus. Mesopleural area without an expanded acropleuron; mesepimeron extending over anterior margin of metapleuron (Fig. 122). All legs with 5 tarsomeres; protibial spur stout and curved; basitarsal comb longitudinal. Fore wing stigmal vein not at a right angle with anterior fore wing margin. Metasoma with syntergum and therefore without an epipygium, convex or (more frequently) strongly sclerotized and carapace-like (Fig. 124).

Discussion. *Asparagobius* Mayr has been consistently recovered as the sister group of *Ormyrus* Westwood /*Ormyrulus* Bouček with strong support in next-generation molecular analysis (Cruaud et al., submitted). In analysis of morphological characters (van Noort et al., in prep.), we acknowledged the close relationship between *Asparagobius* new placement and Ormyridae. We also propose the inclusion of *Hemadas* Crawford new placement (previously classified in Ormocerinae) in the newly defined Ormyridae.

Ormyridae are most frequently confused with Torymidae because both groups tend to have an arched body and enlarged metacoxa, although torymids have a separate epipygium and usually a long and exserted ovipositor in females whereas that of ormyrids is short. Males of the two groups are usually distinguished using habitus features of genera, and in practice can be easily recognized once the habitus of the two families is learned. Pteromalidae have an axillular sulcus in almost all species, but not in some fig associates that are otherwise highly divergent morphologically and not similar to Ormyridae. Epichrysomallidae have distinctly different fore wing venation from Ormyridae, with a longer stigmal vein that is at approximately a right angle with the anterior fore wing margin, and have a shorter marginal and postmarginal vein. Melanosomellidae lack an occipital carina, and otherwise nearly all species differ in having non-metallic coloration versus the usually metallic Ormyridae (except *Hemadas*).



Figures 121–124. 121, 122 *Ormyrus* sp. (Ormyridae) **121** head dorsal view **122** mesosoma lateral view **123** *Hemadas nubilipennis* (Ashmead) (Ormyridae): mesosoma dorsal view **124** *Asparagobius* sp. (Ormyridae): metasoma lateral view.

Acknowledgements

We thank Gary Gibson, Michael Gates, Christer Hansson, John Huber, Ana Dal Molin, Jason Mottern, John Noyes, Andy Polaszek, Alex Gumovsky, Gérard Delvare, Krissy Dominguez, Robert Kresslein, and Ryan Perry for many helpful comments on the classification. We thank Daniel Alejandro Aquino (Museo de La Plata), Fernando H. A. Farache (Rio Verde), Jeremy Frank (Bishop Museum), and Ryan Perry (UC Santa Barbara) for helpful photographs of type specimens. We thank Nicole Fisher and Juanita Rodriguez Arrieta (ANIC, Canberra) as well as Christine Lambkin, Chris Burwell and Susan Wright (QM, Brisbane) for the loan of multiple Australian specimens. We acknowledge the Queensland government for collecting permits (WITK18248017 - WITK18278817). Grant support was provided in part by NSF DEB-1555808 to J. Heraty, J.B. Woolley and M. Yoder. This work was also partly supported by the ANR projects TRIPTIC (ANR-14-CE18-0002), BIDIME (ANR-19-ECOM-0010) and recurring funding of the INRAE to A. Cruaud and J.Y. Rasplus.

References

Ashmead WH (1895) On the genus *Pelecinella*, Westwood, and its position among the Chalcididae. Proceedings of the Entomological Society of Washington 3: 230–233.

Ashmead WH (1899) On the genera of the Cleonymidae. Proceedings of the Entomological Society of Washington 4: 200–206.

Ashmead WH (1904) Classification of the chalcid flies, or the superfamily Chalcidoidea, with descriptions of new species in the Carnegie Museum, collected in South America by Herbert H. Smith. Memoirs of the Carnegie Museum 1: i–xi, 225–551. [pls xxxi–xxxix] https://doi.org/10.5962/bhl.title.10341

Basibuyuk H, Quicke DL (1994) Evolution of antennal cleaner structure in the Hymenoptera (Insecta). Norwegian Journal of Agricultural Sciences Supplement No 16: 199–206.

Böhmová J, Rasplus J-Y, Taylor GS, Janšta P (2022) Description of two new Australian genera of Megastigmidae (Hymenoptera, Chalcidoidea) with notes on the biology of the genus Bortesia. Journal of Hymenoptera Research 90: 75–99. https://doi.org/10.3897/jhr.90.82582

Bouček Z (1988) Australasian Chalcidoidea (Hymenoptera). A biosystematic revision of genera of fourteen families, with a reclassification of species. CAB International, Wallingford, UK, 832 pp.

Burks RA (2012) Formation of family group names using the stem -gaster, with special reference to names based on *Miscogaster* and *Sphegigaster* (Hymenoptera: Chalcidoidea: Pteromalidae). Zootaxa 3389: 61–64. https://doi.org/10.11646/zootaxa.3389.1.7

Burks RA, Heraty JM (2015) Subforaminal bridges in Hymenoptera (Insecta), with a focus on Chalcidoidea). Arthropod Structure & Development 44: 173–194. https://doi.org/10.1016/j.asd.2014.12.003

Burks RA, Krogmann L, Heraty JM (2018) Simultaneous discovery and taxonomic placement of new extant and fossil genera of Herbertiinae (Hymenoptera: Chalcidoidea: Pteromalidae). Insect Systematics and Diversity 2(5): 1–8. https://doi.org/10.1093/isd/ixy012

Campbell B, Heraty J, Rasplus J-Y, Chan K, Steffen-Campbell J, Babcock C (2000) Molecular systematics of the Chalcidoidea using 28S-D2 rDNA. In: Austin AD, Dowton M (Eds) Hymenoptera: Evolution, Biodiversity and Biological Control. CSIRO Publishing, Melbourne, Australia, 59–73. https://doi.org/10.1071/9780643090088

Cruaud A, Rasplus J-Y, Zhang J, Burks R, Delvare G, Fusu L, Gibson GAP, Gumovsky A, Hanson P, Huber JT, Janšta P, Mitroiu M-D, Noyes JS, van Noort S, Baker A, Böhmová J, Baur H, Blaimer BB, Brady SG, Bubeníková K, Chartois M, Copeland RS, Dale-Skey Papilloud N, Dal Molin A, Darling C, Dominguez C, Fisher N, Gates MW, Gebiola M, Guerrieri E, Haas M, Hansson C, Heydon S, Kresslein RL, Krogmann L, Moriarty Lemmon E, Mottern J, Murray E, Nidelet S, Nieves Aldrey JL, Perry R, Peters RS, Pinto JD, Polaszek A, Sauné L, Schmidt S, Torréns J, Triapitsyn S, Tselikh EV, Ubaidillah R, Yoder M, Lemmon A, Woolley JB, Heraty JM (2022) The Chalcidoidea bush of life-a massive radiation blurred by mutational saturation. Submitted. bioRxiv, 1–74. https://doi.org/10.1101/2022.09.11.507458

Darling DC (1988) Comparative morphology of the labrum in Hymenoptera: the digitate labrum of Perilampidae and Eucharitidae (Chalcidoidea). Canadian Journal of Zoology 66: 2811–2835. https://doi.org/10.1139/z88-409

Delvare G, LaSalle J (2000) *Trisecodes* gen. n., (Hymenoptera: Eulophidae: Entedoninae), the first eulophid with three tarsal segments. Journal of Hymenoptera Research 9(2): 305–312.

Desjardins CA, Regier JC, Mitter C (2007) Phylogeny of pteromalid parasitic wasps (Hymenoptera: Pteromalidae): initial evidence from four protein-coding nuclear genes. Molecular Phylogenetics and Evolution 45(2): 454–469. https://doi.org/10.1016/j.ympev.2007.08.004

Desjardins CA (2004) Systematics of Diparinae (Hymenoptera: Pteromalidae), and their position within the broader context of pteromalid phylogeny. PhD Thesis. University of Maryland, College Park, 1–259.

Desjardins CA (2007) Phylogenetics and classification of the world genera of Diparinae (Hymenoptera: Pteromalidae). Zootaxa 1647: 1–88. https://doi.org/10.11646/zootaxa.1647.1.1

Dzhanokmen KA (1986) New genera and species of pteromalids (Hymenoptera, Pteromalidae) from the Soviet Far East. In: Ler PA, Belokobylskii AS, Storozheva NA (Eds) Pereponchatokriliye Vostochnoy Sibiri i Dalinego Vostoka, 49–54.

Gauthier N, LaSalle J, Quicke DLJ, Godfray HCJ (2000) Phylogeny of Eulophidae (Hymenoptera: Chalcidoidea), with a reclassification of Eulophinae and the recognition that Elasmidae are derived eulophids. Systematic Entomology 25: 521–539. https://doi.org/10.1046/j.1365-3113.2000.00134.x

Gibson GAP (1989) Phylogeny and classification of Eupelmidae, with a revision of the world genera of Calosotinae and Metapelmatinae (Hymenoptera: Chalcidoidea). Memoirs of the Entomological Society of Canada 149: 1–121. https://doi.org/10.4039/entm121149fv

Gibson GAP (1995) Parasitic wasps of the subfamily Eupelminae: classification and revision of world genera (Hymenoptera: Chalcidoidea: Eupelmidae). Memoirs on Entomology, International 5: [v +] 421.

Gibson GAP (1997) Annotated Keys to the Genera of Nearctic Chalcidoidea (Hymenoptera) Chapter 2. Morphology and Terminology. In: Gibson GAP, Huber JT, Woolley JB (Eds) National Research Council of Canada, NRC Research Press, Ottawa Canada, 16–44.

Gibson GAP (2003) Phylogenetics and classification of Cleonyminae (Hymenoptera: Chalcidoidea: Pteromalidae). Memoirs on Entomology, International 16: [v +] 339.

Gibson GAP, Heraty JM, Woolley JB (1999) Phylogenetics and classification of Chalcidoidea and Mymarommatoidea - a review of current concepts (Hymenoptera, Apocrita). Zoologica Scripta 28: 87–124. https://doi.org/10.1046/j.1463-6409.1999.00016.x

Gibson GAP, Read J, Huber JT (2007) Diversity, classification and higher relationships of Mymarommatoidea (Hymenoptera). Journal of Hymenoptera Research 16(1): 51–146.

Graham MWR de V (1969) The Pteromalidae of north-western Europe (Hymenoptera: Chalcidoidea). Bulletin of the British Museum (Natural History) (Entomology) Supplement 16: 1–908. https://doi.org/10.5962/p.258046

Grissell EE (1995) Toryminae (Hymenoptera: Chalcidoidea: Torymidae): a redefinition, generic classification and annotated world catalogue of species. Memoirs on Entomology, International 2, 474 pp.

Gumovsky A (2002) Monophyly and preliminary phylogeny of Entedoninae (Hymenoptera, Chalcidoidea, Eulophidae) with notes on related groups: 28S D2 rDNA considerations and morphological support. In: Austin AD, Dowton M (Eds) CSIRO Publishing, Collingwood, Victoria. Parasitic Wasps: Evolution, Systematics, Biodiversity and Biological Control, 193–219.

Gumovsky A, Perkovsky E, Rasnitsyn A (2018) Laurasian ancestors and "Gondwanan" descendants of Rotoitidae (Hymenoptera: Chalcidoidea): what a review of Late Cretaceous *Baeomorpha* revealed. Cretaceous Research 84: 286–322. https://doi.org/10.1016/j.cretres.2017.10.027

Haas M, Burks RA, Krogmann L (2018) A new lineage of Cretaceous jewel wasps (Chalcidoidea: Diversinitidae). PeerJ 6(e4633): 30. https://doi.org/10.7717/peerj.4633

Handlirsch A (1925) Systematische übersicht. In: Handbuch der Entomologie. Gustav Fischer Verlag, Jena, Germany, 711–825.

Hennig W (1950) Grundzuge einer Theorie der phylogenetischen Systematik. Deutscher zentralverlag, Berlin, 370 pp.

Hennig W (1966) Phylogenetic systematics. Urbana, USA. University of Illinois Press, 263 pp.

Heraty JM, Burks RA, Cruaud A, Gibson GA, Liljeblad J, Munro JB, Rasplus J-Y, Delvare G, Janšta P, Gumovsky A, Huber JT, Woolley JB, Krogmann L, Heydon SL, Polaszek A, Schmidt S, Darling DC, Gates M, Mottern J, Murray E, Dal Molin A, Triapitsyn SV, Baur H, Pinto JD, Van Noort S, George JN, Yoder MJ (2013) A phylogenetic analysis of the megadiverse Chalcidoidea (Hymenoptera). Cladistics 29: 466–542. https://doi.org/10.1111/cla.12006

Heraty JM, Darling DC (1984) Comparative morphology of the planidial larvae of Eucharitidae and Perilampidae (Hymenoptera: Chalcidoidea). Systematic Entomology 9: 309–328. https://doi.org/10.1111/j.1365-3113.1984.tb00056.x

Heydon SL (1988) The Sphegigasterini: A cladistic analysis and generic classification with reviews of selected genera (Hymenoptera: Pteromalidae). PhD Thesis. University of Illinois at Urbana-Champaign.

Heydon SL, Hanson PE (2005) A first review of the Coelocybinae of the New World (Hymenoptera: Pteromalidae). Acta Societatis Zoologicae Bohemoslovenicae 69(1–2): 147–166.

Janšta P (2014) Phylogeny of parasitic wasps of Torymidae (Hymenoptera: Chalcidoidea) and evolution of their life-strategies. PhD Thesis. Charles University in Prague.

Janšta P, Cruaud A, Delvare G, Genson G, Heraty J, Křížková B, Rasplus J-Y (2018) Torymidae (Hymenoptera, Chalcidoidea) revised: molecular phylogeny, circumscription and reclassification of the family with discussion of its biogeography and evolution of life-history traits. Cladistics 34: 627–651. https://doi.org/10.1111/cla.12228

Kim I-K, La Salle J (2005) Boucekelimini trib. nov., with genera *Boucekelimus* gen. nov. and *Tatiana* gen. nov. (Hymenoptera: Eulophidae) from Western Australia. Acta Societatis Zoologicae Bohemicae 69: 185–192.

Krogmann L, Vilhelmsen L (2006) Phylogenetic implications of the mesosomal skeleton in Chalcidoidea (Hymenoptera, Apocrita)–tree searches in a jungle of homoplasy. Invertebrate Systematics 20: 615–674. https://doi.org/10.1071/IS06012

Miko I, Vilhelmsen L, Johnson NF, Masner L, Penzes Z (2007) Skeletomusculature of Scelionidae (Hymenoptera: Platygastroidea): head and mesosoma. Zootaxa 1571: 1–78. https://doi.org/10.11646/zootaxa.1571.1.1

Mitroiu M-D (2016) Review of world genera of Ceinae, with the description of two new Palearctic species of *Spalangiopelta* Masi (Hymenoptera, Chalcidoidea, Pteromalidae). European Journal of Taxonomy 251: 1–15. https://doi.org/10.5852/ejt.2016.251

Mitroiu M-D (2017) Revision of world Austroterobiinae and Parasaphodinae (Hymenoptera: Chalcidoidea: Pteromalidae), parasitoids of giant scales (Hemiptera: Coccoidea: Monophlebidae). Zootaxa 4301: 1–63. https://doi.org/10.11646/zootaxa.4301.1.1

Mottern JL, Heraty JM, Hartop E (2011) *Cales* (Hymenoptera: Chalcidoidea): morphology of an enigmatic taxon with a review of species. Systematic Entomology 36(2): 267–284. https://doi.org/10.1111/j.1365-3113.2010.00557.x

Munro JB, Heraty JM, Burks RA, Hawks D, Mottern J, Cruaud A, Rasplus J-Y, Jansta P (2011) A molecular phylogeny of the Chalcidoidea (Hymenoptera). PLoS ONE 6: e27023. https://doi.org/10.1371/journal.pone.0027023

Narendran TC (2001) A new record of the genus *Erotolepsiella* Girault (Hymenoptera: Pteromalidae) from the Oriental region with description of a new species from India. Zoos' Print Journal 16(2): 418–420. https://doi.org/10.11609/JoTT.ZPJ.16.2.418-20

Noyes JS (1990) A word on chalcidoid classification. Chalcid Forum, 6–7.

Noyes JS (2019) Universal Chalcidoidea Database. https://www.nhm.ac.uk/our-science/data/chalcidoids/

Peck O, Bouček Z, Hoffer A (1964) Keys to the Chalcidoidea of Czechoslovakia (Insecta: Hymenoptera). Memoirs of the Entomological Society of Canada 96: 1–121. https://doi.org/10.4039/entm9634fv

Rasnitsyn A, Quicke D, Basibuyuk H (2004) A basal chalcidoid (Insecta: Hymenoptera) from the earliest Cretaceous or latest Jurassic of Mongolia. Insect Systematics & Evolution 35: 123–135. https://doi.org/10.1163/187631204788912391

Rasplus JY, Kerdelhué C, Clainche I, Mondor G (1998) Molecular phylogeny of fig wasps. Agaonidae are not monophyletic. Comptes Rendus de l`Académie des Sciences, Paris (III) (Sciences de la Vie) 321(6): 517–527. https://doi.org/10.1016/S0764-4469(98)80784-1

Rasplus J-Y, Blaimer BB, Brady SG, Burks RA, Delvare G, Fisher N, Gates M, Gauthier N, Gumovsky AV, Hansson C, Heraty JM, Fusu L, Nidelet S, Pereira RAS, Sauné L, Ubaidillah R, Cruaud A (2020) A first phylogenomic hypothesis for Eulophidae (Hymenoptera, Chalcidoidea). Journal of Natural History 54: 597–609. https://doi.org/10.1080/00222933.2020.1762941

Vago J-L (2006) Revision of the collections of Chalcidoidea Pteromalidae (Hymenoptera) of the Belgian Royal Institute of Natural Sciences and the university faculty of agronomic sciences of Gembloux, and the discovery of 145 new species for Belgium. Bulletin de la Société Royale Belge d`Entomologie 142(1–6): 73–99.

Van Noort S, Harten A van (2006) The species richness of fig wasps (Hymenoptera: Chalcidoidea: Agaonidae, Pteromalidae) in Yemen. Fauna of Arabia 22: 449–472.

Walker F (1834) Monographia chalciditum (continued). Entomological Magazine 2: 286–309.

Wiebes JT (1967) Redescription of Sycophaginae from Ceylon and India, with designation of lectotypes, and a world catalogue of the Otitesellini (Hymenoptera: Chalcidoidea, Torymidae). Tijdschrift voor entomologie 110: 399–442.

Zhang J, Heraty JM, Darling DC, Kresslein RL, Baker AJ, Torréns J, Rasplus J-Y, Lemmon AR, Lemmon EM (2022) Anchored phylogenomics and a revised classification of the planidial larva clade of jewel wasps (Hymenoptera: Chalcidoidea). Systematic Entomology 47(2): 329–353. https://doi.org/10.1111/syen.12533

Appendix I

Classification of genera in families discussed here

Boucekiidae: *Boucekius* Gibson, *Chalcidiscelis* Ashmead
Calesidae: *Cales* Howard
Ceidae: *Bohpa* Darling, *Cea* Walker, *Spalangiopelta* Masi
Cerocephalidae: *Acerocephala* Gahan, *Cerocephala* Westwood, *Choetospilisca* Hedqvist, *Dominocephala*† Krogmann, *Gahanisca* Hedqvist, *Gnathophorisca* Hedqvist, *Laesthiola* Bouček, *Muesebeckisia* Hedqvist, *Neocalosoter* Girault & Dodd, *Neosciatheras* Masi, *Paracerocephala* Hedqvist, *Paralaesthia* Cameron, *Pteropilosa*† Bläser, Krogmann & Peters, *Sciatherellus* Masi, *Tenuicornis*† Bläser, Krogmann & Peters, *Theocolax* Westwood
Chalcedectidae: *Chalcedectus* Walker
Cleonymidae: *Agrilocida* Steffan, *Callocleonymus* Masi, *Cleonymus* Latreille, *Dasycleonymus* Gibson, *Notanisus* Walker, *Zolotarewskya* Risbec
Coelocybidae: *Acoelocyba* Bouček, *Ambogaster* Heydon, *Ariasina* Heydon, *Coelocyba* Ashmead, *Coelocyboides* Girault, *Cooloolana* Bouček, *Cybopella* Bouček, *Erotolepsiella* Girault, *Eucoelocybomyia* Girault, *Fusiterga* Bouček, *Lanthanomyia* De Santis, *Lelapsomorpha* Girault, *Liepara* Bouček, *Nerotolepsia* Girault, *Ormyromorpha* Girault, *Paratomicobia* Girault, *Tomicobomorphella* Girault
Diparidae: *Cerodipara* Desjardins, *Chimaerolelaps* Desjardins, *Conodipara* Hedqvist, *Conophorisca* Hedqvist, *Dipara* Walker, *Diparisca* Hedqvist, *Dozodipara* Desjardins, *Hedqvistina* Koçak, Hüseyinoglu & Kemal, *Lelaps* Walker, *Myrmicolelaps* Hedqvist, *Netomocera* Bouček
Epichrysomallidae: *Acophila* Ishii, *Asycobia* Bouček, *Camarothorax* Mayr, *Epichrysomalla* Girault, *Eufroggattisca* Ghesquière, *Herodotia* Girault, *Josephiella* Narendran, *Lachaisea* Rasplus, *Leeuweniella* Ferrière, *Meselatus* Girault, *Neosycophila* Grandi, *Odontofroggatia* Ishii, *Parasycobia* Abdurahiman & Joseph, *Sycobia* Walker, *Sycobiomorphella* Abdurahiman & Joseph, *Sycomacophila* Rasplus, *Sycophilodes* Joseph, *Sycophilomorpha* Joseph & Abdurahiman, *Sycotetra* Bouček
Eulophidae (altered genera only): **Eulophinae**: **Eulophini**: *Elasmus* Westwood. **Opheliminae**: **Boucekelimini**: *Boucekelimus* Kim & La Salle, *Tatiana* Kim & La Salle; **Platytetracampini**: *Platytetracampe* Girault. **Tetrastichinae**: **Tetrastichini**: *Gyrolasomyia* Girault
Eunotidae: *Butiokeras*† Burks & Heraty, *Cavitas* Xiao & Huang, *Cephaleta* Motschulsky, *Epicopterus* Westwood, *Eunotus* Walker, *Mesopeltita* Ghesquière, *Scutellista* Motschulsky

Eupelmidae (altered genera only): **Eusandalinae**: *Archaeopelma* Gibson, *Eusandalum* Ratzeburg, *Licrooides* Gibson, *Paraeusandalum* Gibson, *Pentacladia* Westwood
Herbertiidae: *Exolabrum* Burks, *Herbertia* Howard, *Versolabrum*† Burks & Krogmann
Hetreulophidae: *Hetreulophus* Girault, *Omphalodipara* Girault, *Zeala* Bouček
Heydeniidae: *Heydenia* Förster, *Heydeniopsis*† Hedqvist
Idioporidae: *Idioporus* LaSalle & Polaszek
Lyciscidae: **Lyciscinae**: *Agamerion* Haliday, *Amazonisca* Hedqvist, *Chadwickia* Bouček, *Epistenia* Westwood, *Eupelmophotismus* Girault, *Hadroepistenia* Gibson, *Hedqvistia* Gibson, *Lycisca* Spinola, *Marxiana* Girault, *Mesamotura* Girault, *Neboissia* Bouček, *Neoepistenia* Hedqvist, *Nepistenia* Bouček, *Paralycisca* Hedqvist, *Parepistenia* Dodd, *Proglochin* Philippi, *Proshizonotus* Girault, *Protoepistenia* Gibson, *Riekisura* Bouček, *Romanisca* Hedqvist, *Scaphepistenia* Gibson, *Shedoepistenia* Gibson, *Striatacanthus* Gibson, *Thaumasura* Westwood, *Urolycisca* Roman, *Westwoodiana* Girault. **Solenurinae**: *Grooca* Sureshan & Narendran, *Solenura* Westwood
Macromesidae: *Macromesus* Walker
Megastigmidae (transferred subfamilies only): **Chromeurytominae**: *Asaphoideus* Girault, *Chromeurytoma* Cameron, *Patiyana* Bouček. **Keiraninae**: *Keirana* Bouček
Melanosomellidae: *Aditrochus*, Rübsaamen, *Aeschylia*, Girault, *Alloderma*, Ashmead, *Alyxiaphagus*, Riek, *Australicesa*, Koçak, &, Kemal, *Brachyscelidiphaga*, Ashmead, *Encyrtocephalus*, Ashmead, *Epelatus*, Girault, *Espinosa*, Gahan, *Eurytomomma*, Girault, *Hansonita*, Bouček, *Hubena*, Bouček, *Indoclava*, Gupta,, Khan, &, Agnihotri, *Krivena*, Bouček, *Lincolna*, Girault, *Lisseurytoma*, Cameron, *Mayrellus*, Crawford, *Megamelanosoma*, Girault, *Nambouria*, Bouček, *Neochalcissia*, Girault, *Neoperilampus*, Girault, &, Dodd, *Perilampella*, Girault, &, Dodd, *Perilampomyia*, Girault, *Plastobelyta*, Kieffer, *Queenslandia*, Koçak, &, Kemal, *Systolomorpha*, Ashmead, *Terobiella*, Ashmead, *Trichilogaster*, Mayr, *Westra*, Bouček, *Wubina*, Bouček, *Xantheurytoma*, Cameron
Metapelmatidae: *Metapelma* Westwood
Moranilidae: **Moranilinae**: *Amoturella* Girault, *Aphobetus* Howard, *Australeunotus* Girault, *Australurios* Girault, *Eunotomyiia* Girault, *Globonila* Bouček, *Hirtonila* Bouček, *Ismaya* Bouček, *Kneva* Bouček, *Mnoonema* Motschulsky, *Moranila* Cameron, *Ophelosia* Riley, *Tomicobiella* Girault, *Tomicobomorpha* Girault. **Tomocerodinae**: *Tomocerodes* Girault
Neanastatidae: *Lambdobregma* Gibson, *Neanastatus* Girault
Neodiparidae: **Elatoidinae**: *Elatoides* Nikol'skaya. **Neodiparinae**: *Neodipara* Erdős
Ooderidae: *Oodera* Westwood
Ormyridae: *Asparagobius* Mayr, *Hemadas* Crawford, *Ormyrulus* Bouček, *Ormyrus* Westwood
Pelecinellidae: **Nefoeninae**: *Nefoenus* Bouček. **Pelecinellinae**: *Doddifoenus* Bouček, *Leptofoenus* Smith
Pirenidae: **Cecidellinae**: *Cecidellis* Hanson; **Eriaporinae**: *Eunotiscus* Compere, *Promuscidea* Girault. **Euryischiinae**: *Euryischia* Riley, *Euryischomyia* Girault, *Myiocnema* Ashmead. **Pireninae**: *Ecrizotomorpha* Mani, *Keesia* Mitroiu, *Lasallea*

Bouček, *Macroglenes* Westwood, *Papuaglenes* Mitroiu, *Petipirene* Bouček, *Velepirene* Bouček, *Watshamia* Bouček, *Zebe* La Salle. **Tridyminae**: *Calyconotiscus* Narendran & Saleem, *Ecrizotes* Förster, *Epiterobia* Girault, *Gastrancistrus* Westwood, *Melancistrus* Graham, *Oxyglypta* Förster, *Premiscogaster* Girault, *Sirovena* Bouček, *Spathopus* Ashmead, *Spinancistrus* Kamijo

Pteromalidae: **Colotrechninae**: **Amerostenini**: *Amerostenus* Girault, *Errolia* Bouček, *Glorimontana* Bouček, *Yrka* Bouček; **Colotrechnini**: *Baridobius* Heydon, *Bofuria* Hedqvist, *Bomburia* Hedqvist, *Cameronella* Dalla Torre, *Colotrechnus* Thomson, *Dipachystigma* Crawford, *Dvalinia* Hedqvist, *Elachertodomyia* Girault, *Pachyneuronella* Girault, *Podivna* Bouček, *Uriellopteromalus* Girault, *Uzka* Bouček; **Divnini**: *Divna* Bouček; **Trigonoderopsini**: *Bugacia* Erdős, *Trigonoderopsis* Girault. **Erixestinae**: *Erixestus* Crawford. **Miscogastrinae**: **Diconocarini**: *Diconocara* Dzhanokmen; **Miscogastrini**: *Collentis* Heydon, *Drailea* Huang, *Glyphognathus* Graham, *Lamprotatus* Westwood, *Miscogaster* Walker, *Neoskeloceras* Kamijo, *Paralamprotatus* Liao, *Seladerma* Walker, *Sphaeripalpus* Förster, *Stictomischus* Thomson, *Telepsogina* Hedqvist, *Thektogaster* Delucchi, *Tumor* Huang, *Xestomnaster* Delucchi; **Sphegigastrini**: *Acroclisis* Förster, *Ammeia* Delucchi, *Andersena* Bouček, *Ardilea* Graham, *Bairamlia* Waterston, *Bubekia* Dalla Torre, *Bubekiana* De Santis, *Callicarolynia* Heydon, *Callimerismus* Graham, *Ceratetra* Dzhanokmen, *Cryptoprymna* Förster, *Cyrtogaster* Walker, *Haliplogeton* De Santis, *Halticoptera* Spinola, *Harrizia* Delucchi, *Kazina* Bouček, *Maorita* Bouček, *Mauleus* Graham, *Merismus* Walker, *Notoglyptus* Masi, *Notoprymna* De Santis, *Novitzkyanus* Bouček, *Paracroclisis* Girault, *Ploskana* Bouček, *Polstonia* Heydon, *Rhicnocoelia* Graham, *Schimitschekia* Bouček, *Sorosina* Dzhanokmen, *Sphegigaster* Spinola, *Syntomopus* Walker, *Thinodytes* Graham, *Toxeuma* Walker, *Tricyclomischus* Graham, *Trigonogastrella* Girault, *Vespita* Bouček. **Ormocerinae**: *Blascoa* Askew, *Cecidoxenus* Ashmead, *Monazosa* Dzhanokmen, *Nodisoplata* Graham, *Ormocerus* Walker. **Pachyneurinae**: *Acroclisoides* Girault & Dodd, *Amblyharma* Huang & Tong, *Austroterobia* Girault, *Canada* Koçak & Kemal, *Coruna* Walker, *Euneura* Walker, *Fusta* Xiao & Ye, *Goidanichium* Bouček, *Golovissima* Dzhanokmen, *Inkaka* Girault, *Metastenus* Walker, *Nazgulia* Hedqvist, *Neotoxeumorpha* Narendran, *Oomara* Delucchi, *Oricoruna* Bouček, *Ottaria* Hedqvist, *Pachycrepoideus* Ashmead, *Pachyneuron* Walker, *Parabruchobius* Risbec, *Platecrizotes* Ferrière, *Teasienna* Heydon, *Toxeumorpha* Girault. **Pteromalinae**: **Otitesellini**: *Adiyodiella* Priyadarsanan, *Apocrypta* Coquerel, *Arachonia* Joseph, *Bouceka* Koçak & Kemal, *Comptoniella* Wiebes, *Crossogaster* Mayr, *Diaziella* Grandi, *Dobunabaa* Bouček, *Eujacobsonia* Grandi, *Grandiana* Wiebes, *Grasseiana* Abdurahiman & Joseph, *Guadalia* Wiebes, *Lipothymus* Grandi, *Marginalia* Priyadarsanan, *Micranisa* Walker, *Micrognathophora* Grandi, *Otitesella* Westwood, *Philosycella* Abdurahiman & Joseph, *Philosycus* Wiebes, *Philoverdance* Priyadarsanan, *Philotrypesis* Förster, *Robertsia* Bouček, *Seres* Waterston, *Sycoecus* Waterston, *Sycoryctes* Mayr, *Sycoscapter* Saunders, *Walkerella* Westwood, *Watshamiella* Wiebes; **Pteromalini**: *Ablaxia* Delucchi, *Abomalus* Bouček, *Acaenacis* Girault, *Acroclisella* Girault, *Acroclisissa* Girault, *Acroclypa* Bouček, *Acrocormus* Förster, *Aepocerus* Mayr, *Afropsilocera* Bouček, *Aggelma* Delucchi,

Agiommatus Crawford, *Aiemea* Bouček, *Allocricellius* Yang, *Alticornis* Bouček, *Amandia* Graham, *Amblypachus* De Santis, *Amphidocius* Dzhanokmen, *Angulifrons* Xiao & Huang, *Anisopteromalus* Ruschka, *Ankaratrella* Risbec, *Anogmoides* Askew, *Anogmus* Förster, *Anorbanus* Bouček, *Apelioma* Delucchi, *Apsilocera* Bouček, *Apycnetron* Bouček, *Arachnopteromalus* Gordh, *Arriva* Bouček, *Arthrolytus* Thomson, *Asoka* Bouček, *Atrichomalus* Graham, *Boharticus* Grissell, *Bonitoa* Bouček, *Boucekina* Szelényi, *Brachycaudonia* Ashmead, *Bupronotum* Xiao & Huang, *Caenacis* Förster, *Caenocrepis* Thomson, *Calliprymna* Graham, *Callitula* Spinola, *Canberrana* Bouček, *Capellia* Delucchi, *Catolaccus* Thomson, *Cecidolampa* Askew, *Cecidostiba* Thomson, *Cheiropachus* Westwood, *Chlorocytus* Graham, *Chrysoglyphe* Ashmead, *Coelopisthia* Förster, *Conigastrus* Bouček, *Conomorium* Masi, *Cratomus* Dalman, *Critogaster* Mayr, *Cyclogastrella* Bukovskii, *Cyrtophagoides* Narendran, *Cyrtoptyx* Delucchi, *Dasyneurophaga* Hedqvist, *Delisleia* Girault, *Delucchia* Koçak & Kemal, *Dibrachoides* Kurdjumov, *Dibrachys* Förster, *Diglochis* Förster, *Dimachus* Thomson, *Dinarmoides* Masi, *Dinarmolaelaps* Masi, *Dinarmus* Thomson, *Dineuticida* Bouček, *Dinotiscus* Ghesquière, *Dinotoides* Bouček, *Diourbelia* Risbec, *Dirhicnus* Thomson, *Doganlaria* Koçak & Kemal, *Dorcatomophaga* Kryger, *Elderia* Hedqvist, *Endomychobius* Ashmead, *Epanogmus* Girault, *Epicatolaccus* Blanchard, *Epipteromalus* Ashmead, *Erdoesina* Graham, *Erythromalus* Graham, *Eulonchetron* Graham, *Eumacepolus* Graham, *Eurydinota* Förster, *Eurydinoteloides* Girault, *Eurydinotomorpha* Girault, *Euteloida* Bouček, *Ezgia* Koçak & Kemal, *Fedelia* Delucchi, *Ficicola* Heydon, *Fijita* Bouček, *Frena* Bouček, *Gbelcia* Bouček, *Genangula* Bouček, *Globimesosoma* Xiao & Hui, *Grissellium* Bouček, *Guancheria* Hedqvist, *Gugolzia* Delucchi & Steffan, *Guinea* Koçak & Kemal, *Guolina* Heydon, *Gyrinophagus* Ruschka, *Habritella* Girault & Dodd, *Habritys* Thomson, *Habromalina* Dzhanokmen, *Halomalus* Erdős, *Halticopterella* Girault & Dodd, *Halticopteroides* Girault, *Helocasis* Wallace, *Heterandrium* Mayr, *Heteroprymna* Graham, *Heteroschema* Gahan, *Hillerita* Bouček, *Hlavka* Bouček, *Hobbya* Delucchi, *Holcaeus* Thomson, *Homoporus* Thomson, *Huberina* Bouček, *Hypopteromalus* Ashmead, *Ischyroptyx* Delucchi, *Isocyrtella* Risbec, *Isocyrtus* Walker, *Isoplatoides* Girault, *Jaliscoa* Bouček, *Kaleva* Graham, *Klabonosa* Bouček, *Kratka* Bouček, *Kukua* Bouček, *Kumarella* Sureshan, *Lampoterma* Graham, *Lariophagus* Crawford, *Laticlypa* Bouček, *Lenka* Bouček, *Leodamus* Masi, *Leptomeraporus* Graham, *Licteria* Risbec, *Lomonosoffiella* Girault, *Lonchetron* Graham, *Longinucha* Bouček, *Lyrcus* Walker, *Lysirina* Heydon, *Lyubana* Bouček, *Makaronesa* Graham, *Mazinawa* Bouček, *Megadicylus* Girault, *Merallus* Masi, *Meraporus* Walker, *Merismoclea* De Santis, *Merismomorpha* Girault, *Merisus* Walker, *Mesopolobus* Westwood, *Metacolus* Förster, *Meximalus* Bouček, *Mimencyrtus* De Santis, *Mirekia* Bouček, *Miristhma* Bouček, *Mokrzeckia* Mokrzecki, *Monoksa* Bouček, *Morodora* Gahan, *Muscidifurax* Girault & Sanders, *Nadelaia* Bouček, *Narendrella* Sureshan, *Nasonia* Ashmead, *Neanica* Erdős, *Nedinotus* Bouček, *Neocatolaccus* Ashmead, *Neolyubana* Sureshan, *Neopolycystus* Girault, *Nephelomalus* Graham, *Nikolskayana* Bouček, *Norbanus* Walker, *Nuchata* Bouček, *Oaxa* Bouček, *Obalana* Bouček, *Olchon* Tselikh, *Oniticellobia* Bouček, *Ottawita* Bouček, *Oxyharma* Bouček, *Oxysychus*

Delucchi, *Pandelus* Förster, *Panstenon* Walker, *Paracarotomus* Ashmead, *Paradinarmus* Masi, *Paraiemea* Sureshan & Narendran, *Paroxyharma* Huang & Tong, *Pegopus* Förster, *Peridesmia* Förster, *Perilampidea* Crawford, *Perniphora* Ruschka, *Pestra* Bouček, *Pezilepsis* Delucchi, *Phaenocytus* Graham, *Platneptis* Bouček, *Platypteromalus* Bouček, *Procallitula* De Santis, *Propicroscytus* Szelényi, *Propodeia* Bouček, *Pseudanogmus* Dodd & Girault, *Pseudetroxys* Masi, *Pseudocatolaccus* Masi, *Psilocera* Walker, *Psilonotus* Walker, *Psychophagoides* Graham, *Psychophagus* Mayr, *Pterapicus* Dzhanokmen, *Pterisemoppa* Girault, *Pteromalus* Swederus, *Pterosemigastra* Girault & Dodd, *Pterosemopsis* Girault, *Ptinocida* Bouček, *Pycnetron* Gahan, *Quercanus* Heydon, *Rakosina* Bouček, *Raspela* Bouček, *Rhaphitelus* Walker, *Rhopalicus* Förster, *Rohatina* Bouček, *Roptrocerus* Ratzeburg, *Sceptrothelys* Graham, *Schizonotus* Ratzeburg, *Sedma* Bouček, *Sigynia* Hedqvist, *Sisyridivora* Gahan, *Spaniopus* Walker, *Sphegigastrella* Masi, *Sphegipterosema* Girault, *Sphegipterosemella* Girault, *Spilomalus* Graham, *Spintherus* Thomson, *Spodophagus* Delvare & Rasplus, *Staurothyreus* Graham, *Stenetra* Masi, *Stenomalina* Ghesquière, *Stenoselma* Delucchi, *Stichocrepis* Förster, *Stinoplus* Thomson, *Strejcekia* Bouček, *Synedrus* Graham, *Systellogaster* Gahan, *Szelenyinus* Bouček, *Tachingousa* Tselikh, *Tanina* Bouček, *Tanzanicesa* Koçak & Kemal, *Termolampa* Bouček, *Thureonella* Gijswijt, *Tomicobia* Ashmead, *Toxeumella* Girault, *Toxeumelloides* Girault, *Trichargyrus* Dzhanokmen, *Trichokaleva* Bouček, *Trichomalopsis* Crawford, *Trichomalus* Thomson, *Tricolas* Bouček, *Trimeromicrus* Gahan, *Trinotiscus* Bouček, *Tritneptis* Girault, *Trjapitzinia* Dzhanokmen, *Trychnosoma* Graham, *Tsela* Bouček, *Uniclypea* Bouček, *Urolepis* Walker, *Usubaia* Kamijo, *Veltrusia* Bouček, *Vrestovia* Bouček, *Xiphydriophagus* Ferrière, *Yanchepia* Bouček, *Yosemitea* Bouček, *Zdenekiana* Huggert. **Sycophaginae**: *Anidarnes* Bouček, *Conidarnes* Farache & Rasplus, *Eukoebelea* Ashmead, *Idarnes* Walker, *Neoeukobelea* Lal, Farooqi & Husain, *Pseudidarnes* Girault, *Sycidiphaga* Liu, Rasplus & Huang, *Sycophaga* Westwood. **Trigonoderinae**: *Erdoesia* Bouček, *Eutelisca* Hedqvist, *Gastracanthus* Westwood, *Janssoniella* Kerrich, *Miscogasteriella* Girault, *Neolelaps* Ashmead, *Ogloblinisca* Hedqvist, *Platygerrhus* Thomson, *Plutothrix* Förster, *Trigonoderus* Westwood. ***Incertae sedis* (unplaced to subfamily)**: *Calolelaps* Timberlake, *Hemitrichus* Thomson, *Ksenoplata* Bouček, *Mesolelaps* Ashmead, *Stictolelaps* Timberlake, *Yusufia* Koçak & Kemal

Spalangiidae: **Erotolepsiinae**: *Balrogia* Hedqvist, *Erotolepsia* Howard, *Eunotopsia* Bouček, *Papuopsia* Bouček. **Spalangiinae**: *Playaspalangia* Yoshimoto, *Spalangia* Latreille

Systasidae: **Systasinae**: *Semiotellus* Westwood, *Systasis* Walker. **Trisecodinae**: *Trisecodes* Delvare & LaSalle

***incertae sedis* taxa in Chalcidoidea not placed to family**

Asaphesinae: *Asaphes* Walker, *Coriotela*† Burks & Heraty, *Hyperimerus* Girault
Austrosystasinae: *Austrosystasis* Girault
Ditropinotellinae: *Ditropinotella* Girault
Eopelma Gibson

Enoggerinae: *Ausasaphes* Bouček, *Enoggera* Girault
Keryinae: *Kerya* Bouček
Louriciinae: *Callimomoides* Girault
Micradelinae: *Micradelus* Walker
Neapterolelapinae: *Neapterolelaps* Girault, *Nosodipara* Bouček, *Pseudoceraphron* Dodd
Parasaphodinae: *Parasaphodes* Schulz
Rivasia Askew & Nieves-Aldrey
Storeyinae: *Storeya* Bouček

Genera inquirenda unplaced to family

Elachertoidea Girault, *Eubeckerella* Narendran, *Glyphotoma* Cameron, *Promerisus* Kieffer, *Pyramidophoriella* Hedqvist, *Selimnus* Walker, *Sennia* De Stefani, *Tripteromalus* Kieffer